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(*1958 Meeting*)

Editor

SHERIDAN BAKER

PART I. NATURAL SCIENCE

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PART I. NATURAL SCIENCE

PALEONTOLOGY

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIV, 1959 (1958 Meeting)

LATE CENOZOIC MICROTINE RODENTS FROM WYOMING AND IDAHO

CLAUDE W. HIBBARD
University of Michigan

This paper is one of a series resulting from relatively detailed study of some Pliocene and Pleistocene faunas from the western United States. Co-operative work with Dwight W. Taylor of the United States Geological Survey is aimed at careful stratigraphic collection of associated fossils representing a number of groups of both plants and animals. We believe that such work can significantly advance knowledge of the geologic range and stratigraphic value of many types of fossils. Possibly even more important will be the broader and firmer basis for environmental interpretation of these fossil-bearing deposits. Especially within the Pleistocene epoch and eventually in the Pliocene as well, the development of an inferred climatic sequence may yield information of great value for correlation. The Pleistocene has been shorter than any other epoch and as a consequence the evolutionary changes in faunas are fewer—and of less stratigraphic usefulness—than in the Miocene or Pliocene, for example.

Even the mammals, a relatively rapidly diversifying group, in some instances have not shown clear evidence of evolution within the Pleistocene. Many genera and species have gradually become extinct during the Ice Age, but a large proportion of these may be Pliocene novelties. The microtine rodents, however, stand in striking contrast to such relatively conservative groups as the camels, horses, and pocket-mice. These mice diversified rapidly during the late Cenozoic and developed progressive specializations. These changes, which are of considerable taxonomic value, include several important modifications of teeth and tooth patterns. Some lines of microtines that had rooted cheek teeth gradually lost these roots and developed high-crowned teeth that grew throughout the life of the animal. Other microtines with rooted or ever-growing cheek teeth had cement deposits on their teeth, and some developed an interrupted enamel pattern on the grinding (occlusal) surface.

List of localities.—The fossil voles reported in this paper were

taken at the following places. All locality numbers are in the United States Geological Survey Cenozoic series. Field numbers are in parentheses.

19128 (DWT 406). Owyhee Co., Idaho. Hammett quad. (1948) 1:24000. SW. ¼ Sec. 1, T. 6 S., R. 8 E. 1550′ E., 650′–1050′ N. of SW. corner. 2600′ elev. Abundant shells and fewer of other fossils weathering from fine sand. Most if not all fossils are from a sandy coquina about 6″ thick.

19129 (DWT 407). Owyhee Co., Idaho. Hammett quad. SW. ¼ Sec. 1, T. 6 S., R. 8 E. 1950′ E., 950′ N. to 2200′ E., 525′ N. of SW. corner. 2690′ elev. Fossils from a 15′–20′ interval of tan, fine, cross-bedded sand immediately above a 2′–3′ thick ash bed. This is probably very close to the locality from which Yen (1944) described freshwater mollusks.

19216 (DWT 431). Twin Falls Co., Idaho. Hagerman quad. (1950) 1:24000. NE. ¼ Sec. 20, T. 7 S., R. 13 E. 1100′ W., 775′ S. to 1150′ W., 650′ S. of NE. corner. 3295′ elev. Hagerman formation, 25′ below top. Fossils from fine, micaceous, cross-bedded, gray sand.

19217 (DWT 432). Twin Falls Co., Idaho. Hagerman quad. NE. ¼ Sec. 20, T. 7 S., R. 13 E. 150′ W., 800′ S. of NE. corner. 3115′ elev. Hagerman formation, 205′ below top. Fossils from fine sand and silt exposed on bench on ridge.

20764 (T56-39). Owyhee Co., Idaho. Jackass Butte quad. (1948) 1:24000. NE. ¼ Sec. 15, T. 4 S., R. 2 E. 1925′ W., 1950′ S. of NE. corner. 2515′ elev. Fossils from fine sand exposed on minor bench immediately south of gulch heading on east side Jackass Butte. This is believed to be the type locality of the microtines described by Wilson (1933).

20765 (DWT 540). Twin Falls Co., Idaho. Hagerman quad. SW. ¼ Sec. 28, T. 7 S., R. 13 E. 350′ E., 2100′ N. of SW. corner. 3025′ elev. Hagerman formation. Fossils from higher saddle on south spur of square-nosed butte, from 2′–10′ above a conspicuous, light gray, 2″-thick, platy weathering, carbonaceous clay shale.

20766 (T56-18). Teton Co., Wyoming. Grand Teton National Park sheet (1948) 1:62500. NW. ¼ Sec. 19, T. 42 N., R. 115 W. 1200′ E., 150′ S. of NW. corner. Teewinot formation. Exposure on northwest side of road to Kelly, 2.3 miles from junction of Kelly road with U. S. Highway 187, in road cut beneath mantle of terrace gravel.

20767 (T56-120; FPV-123). Elmore Co., Idaho. Twentymile Butte quad. (1949) 1:24000. NE. ¼ Sec. 27, T. 7 S., R. 11 E. 0′–250′ W., 1550′ S. of NE. corner. 3165′ elev. Hagerman formation. Fossils from sand exposed on gentle slopes on north side of tributary to Rosevear Gulch.

This study reviews the microtines of the following four assemblages:

1. Unnamed assemblage, Middle Pliocene. Teewinot formation, Jackson Hole, Wyoming.

2. Sand Point local fauna, late Pliocene. Unnamed formation, Owyhee Co., Idaho.

3. Hagerman local fauna, early Pleistocene. Hagerman formation, Twin Falls Co., Idaho.

4. Grand View local fauna, Middle Pleistocene. Unnamed formation, Owyhee Co., Idaho.

The material has been partly collected by Taylor, who since 1954 has been studying the late Cenozoic stratigraphy and paleontology of southern Idaho and adjacent areas. Another part of the material was collected personally in 1956, when I visited the areas listed above to see the fossil sites and to examine the Pliocene and Pleistocene succession in the Snake River valley. The third part consists of older material from various sources.

The fossils are in the following institutions: California Institute of Technology collection at the Los Angeles County Museum (CIT); United States Geological Survey (USGS); United States National Museum (USNM); University of California Museum of Paleontology (UCMP); and University of Michigan Museum of Paleontology (UMMP).

List of species.—The following list summarizes the species discussed in this paper and their stratigraphic occurrence.

Microtoscoptes disjunctus (Wilson)

Described originally from the Middle Pliocene Rome local fauna, southeastern Oregon. Additional specimens are recorded herein from the Teewinot formation, Jackson Hole, Wyoming.

Mimomys (*Cosomys*) *primus* (Wilson); Hagerman local fauna.

This vole was first reported from the Coso Mountains local fauna of California.

Nebraskomys? taylori Hibbard, sp. nov.; Hagerman local fauna.

Pliophenacomys idahoensis Hibbard, sp. nov.; Sand Point local fauna.

Pliophenacomys parvus (Wilson); Grand View local fauna.
Pliopotamys indet.; Sand Point local fauna.
Pliopotamys minor (Wilson); Hagerman local fauna.
Ondatra idahoensis Wilson; Grand View local fauna.

Systematic account of the rodents.—The detailed morphologic descriptions of the fossils follow. In addition to the usual information I have given a list of associated species. The molluscan faunas recovered in association with the vertebrates will be reported upon by Dwight W. Taylor. The large amount of fishbones found with the other specimens are being studied by Carter R. Gilbert, a graduate student at the University of Michigan.

Microtoscoptes disjunctus (Wilson)

(Figs. 1 *A–C*)

Goniodontomys disjunctus Wilson, Love, 1956, Wyo. Geol. Assoc. Guidebook, 11th Ann. Field Conf.: 91; Amer. Assoc. Petrol. Geol. Bull., 40: 1910.

The Mongolian form *Microtoscoptes praetermissus* Schaub is distinguished from *M. disjunctus* by its smaller size.

In the collection from the Middle Pliocene of Jackson Hole (USGS loc. 20766) are parts of three left lower jaws. They are quite fragile. Specimen No. 21383 USNM retains the incisor, M_1 and M_2. The anteroposterior occlusal length of M_1 and M_2 (Fig. 1*B*) is 5.25 mm. The ascending ramus is missing. The lower incisor extends posterior to the alveoli of M_3. The incisor, shape of jaw, position of the mental foramen, and dental pattern agree with that of the holotype (No. 1959 CIT).

Specimen No. 21826 USNM, a young adult individual (Fig. 1*C*), is the most complete. The lower incisor extends posterior to M_3 and for some distance upward into the ascending ramus. There is no capsular process or swelling on the labial side of the jaw to indicate where the incisor ends. The mental foramen is situated dorsally on the diastema just anterior to the alveoli of M_1. The greatest height of the crown of M_1 is 1.8 mm. The occlusal length of M_1 and M_2 is 4.5 mm. M_1 consists of a posterior loop which is broadly confluent with the first inner triangle. The second and third triangles are confluent and nearly opposite. They are separated from the first triangle and the anterior loop by a thin connection of enamel that is no thicker than the enamel along the border of the tooth.

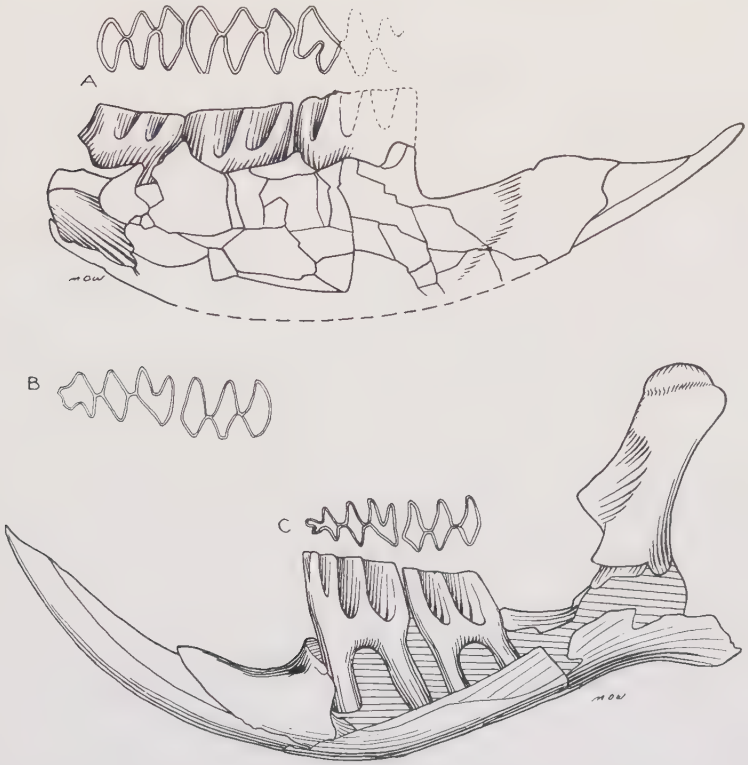

FIG. 1. Lower dentition of *Microtoscoptes disjunctus: A*, USNM 21825, part of left lower jaw, lingual and occlusal views, × 6; *B*, USNM 21383, occlusal view of left M_1 and M_2, × 6; *C*, USNM 21826, part of left lower jaw, labial and occlusal views, × 5.

This thin enamel connection extends to the base of the crown and is transparent. The dentine is confined entirely to the loops and confluent triangles in all the lower molars. The anterior loop consists of the fourth and fifth confluent triangles and a grooved anterior part. The anterior groove of the loop would soon disappear with wear.

M_2 consists of a posterior loop, two confluent and opposite triangles, and an anterior loop.

The masseteric crest of the mandible is present on part of the specimen. It extends posterior to M_2, but due to the broken con-

dition of the jaw the entire length is unknown. The position and development of the part of the masseteric crest which is present is like that in later microtines.

Specimen No. 21825 USNM is broken just posterior to M_3. The anterior part of the crown of M_1 is missing. The incisor passes from the lingual side of the jaw to the labial side just posterior to M_2 and beneath M_3. The posterior part of the incisor is broken, but it extends a short distance past M_3. M_3 consists of a posterior loop, two confluent and opposite triangles, and an anterior loop. The posterior loop and the anterior loop are separated from the two confluent and opposite triangles by a very thin enamel connection (Fig. 1*A*). M_1, M_2, and M_3 have two well-developed roots with the posterior root being larger. The anteroposterior length of M_1–M_3 is 7.0 mm. The occlusal length of M_2 is 2.3 mm. and of M_3, 2.0 mm. Cement is lacking in the re-entrant angles.

Discussion.—A larger series of specimens from both Oregon and Wyoming may show that the Wyoming form is a different species. I consider the difference in the anterior loop between the Oregon and Wyoming specimens as only individual variation, since the anterior loop varies greatly within any given species of microtines. The "Prismenfalte" of Schaub (1940, p. 73; Hinton, 1926, p. 111) as shown by Wilson (1937a, pl. 2, fig. 2) to be present in *M. disjunctus* is absent in the Wyoming specimens. The "prism fold" does not occur in all the young specimens of *Ogmodontomys* but is a variable character.

The genus *Microtoscoptes* was described from the Pliocene of Mongolia by Schaub, who discussed its relationship with the Microtinae. Wilson, not knowing of Schaub's work, described the genus *Goniodontomys*, based upon specimens from the Middle Pliocene of Oregon (Rome local fauna). He considered the specimens as questionably belonging to the Microtinae. Schaub (1934), Stehlin and Schaub (1951), and Wilson (1937a) discussed the relationship of this genus to other rodents. I agree with Schaub and Wilson that its closest affinity is with the Microtinae. A skull or palate with the upper dentition of this rodent would contribute much to the understanding of this genus. Wilson (1937b, p. 51) stated "*Goniodontomys*, if a vole, is an aberrant member of the group without descendants."

Professor Schaub kindly loaned excellent figures of the genotype, which aided greatly in the present study.

Associated forms.—The shrew, *Hesperosorex lovei* Hibbard (1958b), and the beaver, *Dipoides stirtoni* Wilson (Love, 1956b), were found with the remains of *Microtoscoptes disjunctus*. The molluscan fauna, consisting of thirteen species, was reported by Taylor (1956).

Mimomys (*Cosomys*) *primus* (Wilson)

(Figs. 2 *A–E*)

Cosomys primus Wilson, 1932, Jour. Mammal., 13 (2): 150–154, 1 pl.
Mimomys (*Cosomys*) *primus* (Wilson), Wilson, 1933, Carnegie Inst. Wash. Pub., 440: 126–128, 1 fig.

Wilson (1933) gave an excellent description of the parts of this vole recovered from the type Hagerman formation, near the Hagerman horse quarry (Gazin, 1936). He also discussed the probable relationship of the American form with the European genus *Mimomys*.

Many specimens of this vole were recovered by Dwight W. Taylor in the summer of 1955, and by myself in the summer of 1956, from the following two locations in the type Hagerman formation south of the Hagerman horse quarry (N. ½ NW. ¼ Sec. 16, T. 7 S., R. 13 E., Twin Falls County, Idaho): (1) USGS Cenozoic Locality 19217; and (2) Locality 20765. Study of this additional material contributes to the understanding of variation in the species due to age and individual differences.

Five complete lower dentitions were found. The occlusal length of M_1–M_3 is 7.0, 7.0, 7.1, 7.2, and 7.3 mm. Forty-four parts of lower jaws containing M_1 to M_2 were studied. The occlusal length of M_1–M_2 varied from 5.0 to 5.8 mm.; the average is 5.29 mm. Seventy-four first lower molars were examined. Twenty-eight had a shallow pit on the anterior loop (Fig. 2*D*). Two molars were from young specimens that lacked both the pit and "prism fold." The pit soon disappears with wear. An immature RM_1 (Fig. 2*C*) shows the development of the pit from the third outer re-entrant angle. The "prism fold" of Hinton (1926, p. 111) is retained longer than the pit but it disappears in teeth due to wear (Figs. 2 *A–B*). The "prism fold" or evidence of it was present on 51 of the first lower molars.

The posterior end of the lower incisor ends above the dental foramen in a well-developed capsular process on the labial side of the jaw. The dorsal surface of the process is separated from the condylar process by a distinct groove (Figs. 2 *A–B*).

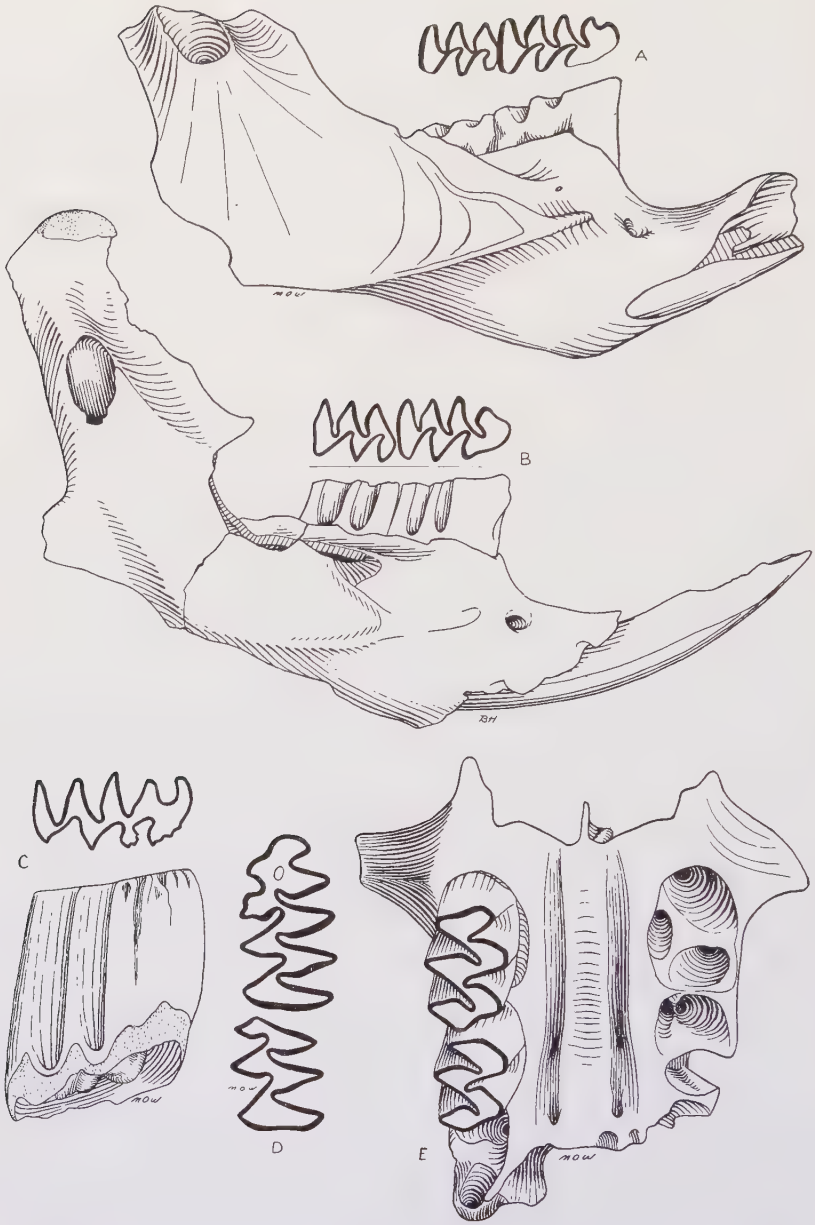

FIG. 2. *Mimomys* (*Cosomys*) *primus: A*, UMMP 34438 and *B*, USNM 21869, right jaws, M_1–M_2, labial and occlusal views, × 10; *C*, UMMP 34204, immature RM_1, labial and occlusal views, × 8; *D*, USNM 21870, left M_1–M_2, occlusal view, × 8; *E*, USNM 21868, palatal view, × 6.

Numerous isolated upper molars were examined. All upper first molars have three well-developed roots except one in which the anterior root is very broad and shows evidence of the fusion of two roots. M^2 is three-rooted and M^3 two-rooted. There is no evidence of cement on any of the teeth. Part of a palate, No. 21868 USNM, with RM^1 and M^2 was taken at Locality 20765 (Fig. 2*E*). The palate terminates more posteriorly than in *Ogmodontomys* and *Pliophenacomys*. It ends opposite the posterior edge of the anterior root of M^3. In the succeeding genera the palate ends approximately at the posterior border of M^2. The most posterior palatine foramina open into the posterolateral pits.

Dwight W. Taylor and Harold E. Malde collected a number of isolated teeth of this vole, November 11, 1956, in Elmore County, Idaho, at USGS Cenozoic Locality 20767. The fossils were taken from an olive drab, medium to coarse grained sand resting on a cinder bed at an elevation of 3,165 feet. Taken in association with these vole teeth were fragments of fish, a frog or toad vertebra, a bird vertebra, a fragment of a large shrew jaw, and part of a left lower jaw of *Canimartes?* cf. *cookii* (Gazin) with M_1 (see Gazin, 1934a and 1937).

Associated forms.—At Locality 20765 *Mimomys* (*Cosomys*) *primus* was found with *Blarina gidleyi* Gazin, *Pliopotamys minor* (Wilson), *Mustela gazini* Hibbard (1958d), *Peromyscus?*, rabbit, gopher, swan, cormorant, *Kinosternon*, *Chrysemys* or *Pseudemys*, catfish, and *Lithoglyphus*. At Locality 19217 *Mimomys primus* occurred with *Blarina gidleyi* Gazin, *Pliopotamys minor* (Wilson), *Chrysemys* or *Pseudemys*, *Gonidea*, *Sphaerium*, *Valvata humeralis* Say, and *Lithoglyphus*. For other members of the Hagerman local fauna see Gazin, 1936.

Discussion.—Although *Mimomys* (*Cosomys*) *primus* is known from only a few localities, nevertheless there is a suggestion that it did not live in the Hagerman area during all of the time in which the Hagerman formation was being deposited. Two sites in the uppermost Hagerman formation have been reasonably well sampled: the horse quarry (elevation, 3,290–3,300 feet) and Locality 19216 (elevation, 3,295 feet). *Mimomys* (*C.*) *primus* has not been found at either of these localities but has been found at several stratigraphically lower. At Locality 19216 a smaller vole, *Nebraskomys? taylori* Hibbard, sp. nov., occurs instead of *Mimomys*. In considering

these occurrences one must bear in mind that they are all in one depositional unit, without intervening unconformities or lithologic changes. I have no explanation for the absence of this vole and the occurrence of another in the uppermost Hagerman formation except environmental change or ecologic replacement or both. It may be entirely due to a local environmental condition. For example, after twenty years of collecting of the Rexroad local fauna at Locality 3 in Meade County, Kansas, only the remains of *Ogmodontomys* have been found at this site. At the Fox Canyon site in Meade County, parts of 1,560 individuals of *Pliophenacomys* have been recovered in comparison to 114 of *Ogmodontomys*. This count is based on the number of left M_1's recovered. The difference in the Rexroad fauna at these two sites appears to be caused by dissimilar local environmental conditions.

I have followed Wilson in considering *Cosomys* as a subgenus of *Mimomys*. The genus *Mimomys* has been used in Europe in the broadest sense to include numerous medium-sized voles with different stages of root development of the teeth, with presence or absence of cement, and with highly specialized pit development of the teeth. The genus as so used is not comparable to genera of recent microtines. A refinement of the usage of the genus *Mimomys* in Europe would help greatly in the stratigraphic study of faunas in that region and would aid in the correlation of faunas between North America and Europe.

Nebraskomys? taylori Hibbard sp. nov.

(Figs. 3 *A–C*)

Holotype.—No. 21832 USNM, part of a right lower jaw with incisor, M_1–M_3. Collected by Dwight W. Taylor in 1955.

Paratypes.—No. 21833 USNM is part of a right lower jaw with incisor, M_1 and M_2; No. 21871 USNM is assigned to parts of two left lower jaws containing the incisor and M_1, and to part of a left lower jaw containing the incisor and M_2. No. 33903 UMMP is a nearly perfect left lower jaw with incisor, M_1 and M_2; and No. 34827 UMMP is part of a right lower jaw with incisor and M_2. Collected in 1956 by Claude W. Hibbard.

Horizon and type locality.—Near the top of the Hagerman formation; Hagerman local fauna, early Pleistocene, tentatively considered as Aftonian. USGS Genozoic Locality 19216, NE. ¼ Sec.

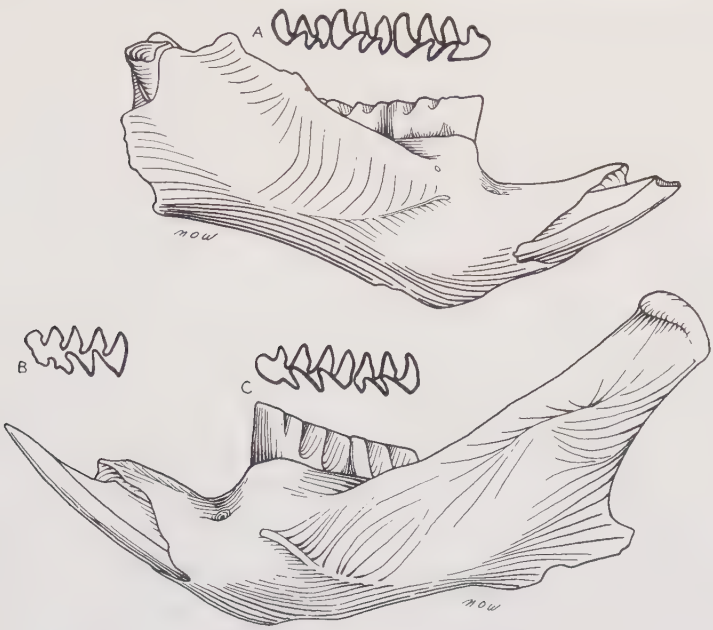

FIG. 3. *Nebraskomys? taylori*, sp. nov.; *A*, USNM 21832, holotype, right jaw, M_1–M_3, labial and occlusal views; *B*, USNM 21871, paratype, left M_1, occlusal view; *C*, UMMP 33903, paratype, left jaw, M_1–M_2, labial and occlusal views. All × 5.

20, T. 7 S., R. 13 E., Twin Falls County, Idaho; Hagerman quadrangle; 1,000 feet W. and 700 feet S. of NE. corner. Fossils from micaceous, cross-bedded, gray, fine sand on ridge at elevation 3,295 feet. This species is only known from the type locality.

Diagnosis.—Nebraskomys? taylori is a vole with rooted molars which lack cement. M_1 consists of a posterior loop, three alternating closed triangles, and a complicated anterior loop. It is larger than *N. mcgrewi* Hibbard and smaller than *Mimomys* (*Cosomys*) *primus* (Wilson). The capsular process for the reception of the incisor is poorly developed.

Description of holotype.—The right lower jaw is that of an adult. It is broken at the ventral border of the dental foramen. The lower incisor is narrower than that of *Mimomys* (*Cosomys*) *primus* and broader than that of *Nebraskomys mcgrewi*. It passes from the lingual side to the labial side of the jaw beneath the posterior root of

M_2. There is no pit between M_3 and the ascending ramus. The mental foramen is situated high on the side of the jaw (Fig. 3*A*) but more anteriorly than in *N. mcgrewi*.

M_1 consists of a closed posterior loop, three alternating closed triangles, and a large anterior loop. There is no evidence of a "prism fold." The re-entrant angles are broad, and the apex of each angle is not as constricted or directed as sharply anteriorly as in *Mimomys* (*C.*) *primus*. The enamel thins slightly in the apex of the re-entrant angles of M_1 and M_2.

M_2 has a closed posterior loop and four alternating triangles. The first and second are closed, and the third and fourth are confluent.

M_3 has a closed posterior loop which is more rounded on the lingual side than (observed) in *Mimomys* (*C.*) *primus* of a comparable stage of wear. The first and second alternating triangles are connected by a narrow tract of dentine. The second lingual or third alternating triangle is closed off from the anterior loop. The apex of each re-entrant angle of M_3 is not directed as strongly forward as in *M.* (*C.*) *primus*. The lower molars are two-rooted. The occlusal length of M_1–M_3 is 5.75 mm. The occlusal length of M_1 is 2.5 mm., and the greatest width is 1.25 mm. The occlusal length of M_2 is 1.75 mm. and of M_3, 1.5 mm. The occlusal length of M_1 of the holotype of *Nebraskomys mcgrewi* is 2.25 mm.

This species is named for Dwight W. Taylor.

Description of paratypes.—No. 21833 USNM is part of a right lower jaw of an adult specimen but younger than that of the holotype. The pattern of M_1 and M_2 agrees with that of the holotype. The occlusal length of M_1 and M_2 is 4.25 mm. The occlusal length of M_1 is 2.5 mm. No. 21871 USNM consists of parts of three right lower jaws, one containing M_2, and the others, M_1. The occlusal pattern of these teeth, except one M_1, agrees with that of the holotype, and of paratype No. 21833. One M_1 (Fig. 3*B*) of an adult individual with age wear comparable to paratype No. 21833, has a very shallow "prism fold." The other paratype with only M_1 is that of a young adult. There is no evidence of the "fold" or a pit on the anterior loop of M_1. Paratype No. 33903 UMMP is that of an adult with a nearly perfect lower jaw (Fig. 3*C*). Only M_1 and M_2 are present. They are in a young adult stage of wear. The occlusal pattern is like that of specimen No. 21833 USNM. There is no evidence of a "prism fold." In teeth with comparable stage of wear

of *Mimomys* (*Cosomys*) *primus* the "prism fold" is present in nearly all specimens.

In specimen No. 33903 UMMP the incisor extends slightly dorsal to the dental foramen but not as high as in *Mimomys* (*C.*) *primus*. Furthermore, the capsular process is not as well developed as in *M.* (*C.*) *primus* (see Figs. 2*A* and *B*). The capsular process is poorly developed as in *Ogmodontomys poaphagus* Hibbard and *Pliophenacomys primaevus* Hibbard. The condyle of the lower jaw of *M.* (*C.*) *primus* above the capsular process for the reception of the incisor is more lingually inflected than that of *Nebraskomys? taylori*.

Two isolated upper first molars were found. Both have three roots; the middle or lingual root is not as well developed for the size of the tooth as is the lingual root of M^1 in *Mimomys* (*Cosomys*) *primus*.

In the Museum of Paleontology, University of California, is part of a right lower jaw, with the incisor and M_2, No. 45063, of this rodent from the type locality. The size and pattern of M_2 is like that of the type and paratypes.

Associated forms.—The following were associated with *Nebraskomys? taylori*: *Blarina gidleyi* Gazin; *Thomomys gidleyi* Wilson; *Alilepus? vagus* Gazin; and *Pliopotamys minor* (Wilson).

Discussion.—I consider *Nebraskomys? taylori* distinct from the genus *Mimomys* for the following reasons: (1) the "prism fold" of M_1 is not a common character; (2) the anterior loop of M_1 lacks the pit or enamel islet; (3) the re-entrant angles of M_1 and M_2 are broad and not directed as strongly forward; (4) the capsular process for the reception of the incisor is poorly developed; and (5) the condyle of the lower jaw is not greatly deflected lingually.

The vole is questionably referred to the genus *Nebraskomys* which occurs in the Sand Draw local fauna of late Nebraskan age (McGrew, 1944; Taylor, 1954; Hibbard, 1957). Skull or palate with teeth, as well as immature dentitions, are needed of both the Hagerman form and *N. mcgrewi* before their true relationship to other Cenozoic voles is known.

Pliophenacomys idahoensis Hibbard sp. nov.

(Figs. 4 *A–I*)

Holotype.—No. 21872, USNM a right M_1. Collected by Dwight W. Taylor in 1956.

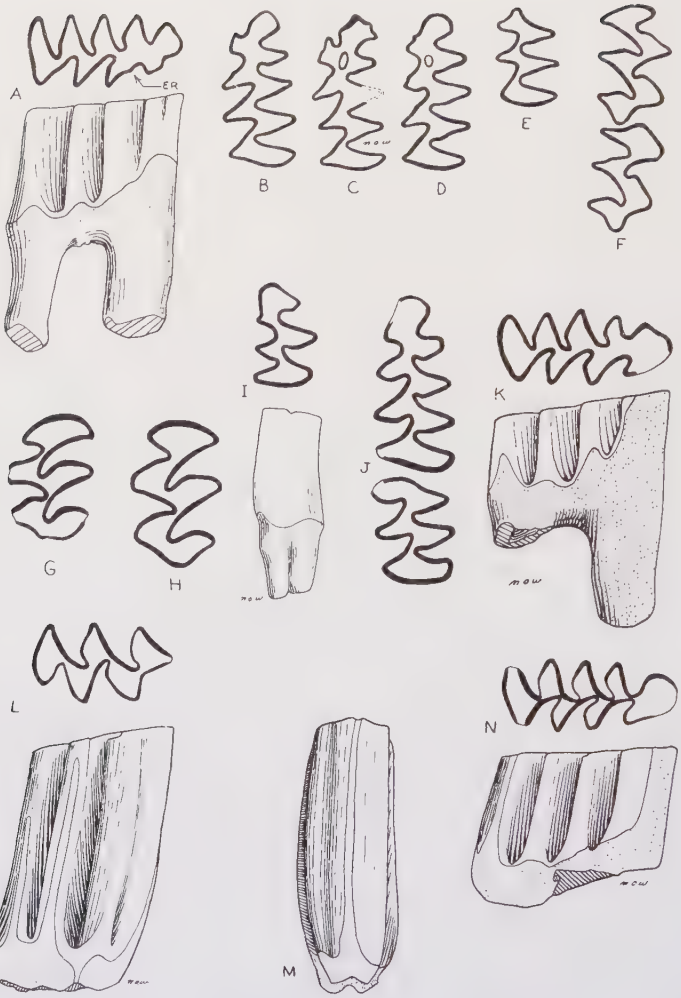

FIG. 4. *Pliophenacomys* and *Pliomys: A*, *Pliophenacomys idahoensis*, sp. nov., holotype, USNM 21872, right M_1, labial and occlusal views; er = enamel ridge. *B–I*, *P. idahoensis*, sp. nov., paratypes; *B–D*, USNM 21873, three left M_1's, occlusal views. *E*, USNM 21874, left M_2, occlusal view. *F*, USNM 21876, right M^1 and M^2, occlusal view. *G* and *H*, USNM 21874, left M^1's, occlusal view. *I*, USNM 21875, left M^3, anterior and occlusal views. *J* and *K*, *P. parvus* (Wilson), USNM 21877; *J*, left M_1 and M_2, occlusal view. *K*, right M_1, labial and occlusal views. *L–N*, *Pliomys episcopalis bolkayi*, UMMP 34901; *L*, left M^1, lingual and occlusal views; *M*, left M^1, posterior view. *N*, right M_1, labial and occlusal views. All × 8.

Paratypes.—No. 21873 USNM includes three left M_1's of young adult and adult specimens; No. 21874 USNM includes two upper left first molars and a left M_2; No. 21875 USNM is two M^3's; and 21876 USNM is part of a right maxillary with M^1 and M^2. Collected in 1956 by Dwight W. Taylor, Harold E. Malde, and Claude W. Hibbard.

Horizon and type locality.—Late Pliocene, USGS Cenozoic Locality 19128, S. ½ SW. ¼ Sec. 1, T. 6 S., R. 8 E., Owyhee County, Idaho; Hammett quadrangle; 1,550 feet E. and 650–1,050 feet N. of the SW. corner of Sec. 1; elevation, 2,600 feet. The formation is unnamed.

Diagnosis.—A small vole slightly smaller than *Pliophenacomys primaevus* Hibbard and distinguished from the latter by narrower re-entrant angles of M_1. The apexes of these angles are slightly constricted and are directed more strongly anteriorly. *Pliophenacomys idahoensis* is smaller than *P. parvus* (Wilson) and *P. meadensis* Hibbard. M_1 of *P. idahoensis* has a small enamel ridge along the anterior face of the second outer (labial) triangle; a vestigial sixth alternating triangle (third labial triangle) forms part of the anterior loop. Its apex (labial edge) is flattened and not pointed as in *P. primaevus*.

Description of holotype.—No. 21872 USNM is an isolated right M_1 of an adult individual. The two roots are well developed. M_1 consists of a posterior loop, five alternating triangles, and an anterior loop. A thin tract of dentine connects the posterior loop and the first three alternating triangles. The fourth and fifth triangles are confluent and open widely into the anterior loop (Fig. 4*A*). A narrow enamel ridge occurs on the anterior face of the second outer triangle. It extends to the base of the re-entrant angle. The flattened apex of the sixth triangle on the labial side of the anterior loop is well developed. The development of the enamel ridge along the anterior face of the second labial triangle has been observed in only one other specimen of *Pliophenacomys* studied. This was on No. 32051d UMMP, an isolated right M_1 of *P. meadensis* from the Dixon local fauna of Kansas. This M_1 also had the flat apex of the sixth triangle (see Hibbard, 1956, fig. 6*D*).

The lingual re-entrant angles of M_1 are narrower than those of *Pliophenacomys primaevus*. There is a tendency for a slight constriction (narrowing) near the apex. The first lingual re-entrant

angle swings slightly forward. The second and third lingual re-entrant angles swing more sharply forward as in *P. meadensis* and *P. parvus.*

The enamel on the anterior loop of M_1 extends downward on a level with the base of the anterior re-entrant angles as in *Pliophenacomys primaevus* and *P. meadensis.* The enamel on the anterolabial side of the anterior loop in *P. parvus* extends well above the base of the anterior re-entrant angles. In wear the anterior loop of *P. parvus* presents an interrupted enamel pattern before the tooth is worn down to the base of the crown. *Pliophenacomys idahoensis* has shorter crowned molars than *P. parvus* and *P. meadensis.*

The occlusal length of M_1 is 2.5 mm. The greatest occlusal width is 1.25 mm.

Descriptions of paratypes.—No. 21873 USNM is a left M_1, with an occlusal length of 2.5 mm. The tooth is from a slightly younger vole than the holotype although the occlusal pattern is the same (Fig. 4*B*). The other two left first lower molars are from younger animals. Their occlusal lengths are 2.5 and 2.6 mm. The occlusal pattern is like that of the other two molars except that there is a very shallow enamel pit (Figs. 4 *C–D*) between the apexes of the fourth lingual and third labial re-entrant angles. Whether this is a common character in young specimens of this species is unknown. It is the first time I have even seen an enamel pit developed in relation to the anterior loop of M_1 in *Pliophenacomys.*

M_2, No. 21874 USNM, is two-rooted and consists of a posterior loop, two alternating triangles, and an anterior loop (Fig. 4*E*). No isolated lower third molars were found. In the collection is part of a badly eroded left lower jaw. It contains the two roots of M_1, M_2, which is worn down to the base of the crown, and the alveoli of M_3, which show that it was two-rooted.

Three isolated upper first molars were taken. All have three well-developed roots. The occlusal length of these teeth are 2.2, 2.2, and 2.3 mm. (Figs. *G–H*). Figure *G* is the occlusal view of the tooth of an old adult that has worn down to the base of the crown.

Two isolated upper third molars, No. 21875 USNM, are in the collection. The occlusal pattern (Fig. 4*I*) is more similar to *Pliophenacomys meadensis* than to that of *P. primaevus.* All teeth are without cement.

Part of a right maxillary, 21876 USNM, of an immature individual containing M^1 and M^2 (Fig. 4*F*) was recovered at USGS Locality 19129, stratigraphically about 100 feet higher than the type locality. In this specimen M^1 is three-rooted, M^2 has the two anterior roots fused. The fusion is well defined by a deep groove along the anterior face of the root. One other isolated M^2 was found. The two most anterior roots were also fused, and a groove is developed along the anterior surface of the root. This is a more advanced character than found in *Pliophenacomys primaevus* where M^2 possesses three well-developed roots.

Sand Point local fauna.—The term Sand Point local fauna is applied here to the fossils from USGS Locality 19128, SW. ¼ Sec. 1, T. 6 S., R. 8 E., Owyhee Co., Idaho. The site is southeast of the town of Hammett, on the south side of the Snake River by Wilson Grade. The "promontory" is locally called Sand Point; whence the name.

Fossils from one other locality, USGS 19129, are referred to the Sand Point local fauna at this time. Locality 19129 is on Sand Point also, but 100 feet topographically and stratigraphically higher. Dwight W. Taylor has furnished the partial list of mollusks from the Sand Point local fauna.

Locality 19128 has yielded a number of mammals, as well as many fishes and mollusks:

MAMMALIA

Hypolagus
Pliophenacomys idahoensis Hibbard sp. nov.
Pliopotamys
Thomomys
Plesippus
mastodont

MOLLUSCA

Sphaerium idahoense Meek
Valvata humeralis Say
Lithoglyphus occidentalis (Hall)
Lithoglyphus superbus (Yen)
Lithoglyphus n. sp.
Fluminicola weaveri Yen
Bithynia campbelli (Dall)
Pyrgulopsis carinata Yen
Ceriphasia taylori (Gabb)
Ceriphasia n. sp.
Lymnaea cf. *stagnalis* (Linné)
Payettia dallii (White)
Anisus pattersoni (Baker)
Gyraulus parvus (Say)
Gyraulus (*Idahoella*) *multicarinatus* (Yen)
Promenetus umbilicatellus (Cockerell)
Ancylus
Orygoceras arcuatum Dall
Hawaiia minuscula (Binney)

Locality 19129 has yielded only one mammal, but a number of mollusks and fishes.

MAMMALIA

Pliophenacomys idahoensis Hibbard, sp. nov.

MOLLUSCA

Gonidea coalingensis Arnold
Valvata humeralis Say
Amnicola bithynoides Yen
Fluminicola weaveri Yen
Lithoglyphus occidentalis (Hall)
Lithoglyphus superbus Yen
Pliopholyx n. sp.
Ceriphasia taylori (Gabb)
Payettia dallii (White)
Gyraulus (*Idahoella*) *multicarinatus* (Yen)
Vorticifex n. sp.
Ancylus
Orygoceras arcuatum Dall

Age of the Sand Point local fauna.—The Sand Point local fauna is probably of latest Pliocene age and seems to be younger than the Rexroad local fauna of Kansas, for the following reasons:

1. *Pliophenacomys idahoensis* is more advanced than *P. primaevus* of the Rexroad local fauna, but less advanced than *P. parvus* of the Grand View local fauna. Unfortunately, no *Pliophenacomys* is known from the Hagerman local fauna.

2. *Pliopotamys* is not known from the Rexroad or the Saw Rock Canyon faunas on the Plains, but appears first in early Pleistocene assemblages. This may be entirely a case of faunal lag if *Pliopotamys* is a northern element that did not reach the southern Plains until a southward shift of the northern fauna during the beginning of the Pleistocene. There are other northern elements that did not reach the southern Plains region until the early Pleistocene, such as *Anisus pattersoni* (Baker), which is known from the Middle Pliocene Teewinot formation, Jackson Hole, Wyoming, and from the late Pliocene Sand Point local fauna. The earliest records of its occurrence in Plains faunas are in the early Pleistocene Sand Draw local fauna of Nebraska and the Dixon local fauna of Kansas. In both of these faunas this mollusk is associated with *Pliopotamys*.

3. The mollusks of the Sand Point local fauna include many extinct species and genera not found in the overlying Hagerman formation. The magnitude of the faunal break is most reasonably explained by postulating the extinction of these groups by changes associated with the beginning of widespread glaciation.

4. Although superposition of the containing stratigraphic units shows that the Hagerman local fauna is younger than the Sand

Point local fauna, the argument may be presented that the differences are only in environments affecting the mollusks, and there may be no significant hiatus between the assemblages. There is, however, sufficient overlap between the types of facies represented that Taylor believes such an explanation inadequate. Furthermore, occurrence in the Sand Point local fauna of a distinct *Pliophenacomys* is suggestive of a definite stratigraphic break. More mammals from the older assemblage will probably help resolve the matter.

5. *Plesippus* certainly does not indicate a necessarily Pleistocene age, if that epoch be defined by the beginning of continental glaciation. In southwestern Kansas, where knowledge of Pliocene and Pleistocene faunal and stratigraphic sequence is more detailed than elsewhere in North America, *Plesippus* is found in three superposed stratigraphic units. The oldest unit, the Rexroad formation, contains three fossil assemblages of markedly Pliocene appearance, both by the relationships of many members of the faunas and by the environmental implications of these assemblages. In the overlying Ballard (Hibbard, 1958a) and Crooked Creek formations the fossils compose markedly different assemblages. They show appearance of many new types of animals and lack great numbers of the Rexroad formation forms. Environmental interpretation of these faunas suggests strongly a marked cooling of the climate, most reasonably correlated with continental glaciation. *Plesippus* is found throughout the two older formations and in the Stump Arroyo member of the Crooked Creek formation (Hibbard, 1949), but the associated small mammals, amphibians, reptiles, and mollusks agree in providing evidence of a sharp faunal break (Hibbard, 1958c; Taylor, in press; Tihen, 1955).

Farther south in the High Plains also, there is another occurrence of *Plesippus* probably of late Pliocene age. At a locality southwest of Channing, Texas (described by Taylor, in press), *Plesippus* is associated with a fauna similar to the Rexroad local fauna. The stratigraphic sequence has not been studied as yet, but the fauna as a whole is in marked contrast to known early Pleistocene assemblages in Texas, Oklahoma, and Kansas.

The Benson local fauna of Arizona includes a horse of the genus *Plesippus* (Gazin, 1942, p. 495). Here, too, other mammals in the fauna suggest a Pliocene age. Savage (1955) has indicated the differences found in *Stegomastodon*, where less advanced types are found

in the Rexroad and Benson local faunas and more advanced kinds in known early Pleistocene assemblages. A gopher in the Benson fauna is most closely related to one of the Rexroad local fauna (Hibbard, 1950, p. 138).

There are other localities for *Plesippus* in North America, such as some in California that are considered as late Pliocene (Woodring, 1952). What I want to emphasize is that the Sand Point *Plesippus* is far from being the only occurrence for which the evidence favors a Pliocene age; and that if *Plesippus* is taken as indicating Pleistocene age a good deal of opposing evidence from various sources is subordinated to one "index fossil."

Pliophenacomys parvus (Wilson)

(Figs. 4 *J–K*)

Mimomys? parvus Wilson, 1933, Carnegie Inst. Wash. pub., No. 440: 128–132, figs. 5 and 6.

Pliophenacomys parvus (Wilson); Hibbard, 1950, Univ. Mich. Mus. Pal., Contrib., 8(6): 155–157.

Pliomys parvus (Wilson) *non* Hibbard; Kretzoi, 1955, Acta Geol., 3 (4): 354.

A member of the Grand View local fauna, *Pliophenacomys parvus* is so far only known from the type locality (USGS 20764). This locality is in the NE. ¼ Sec. 15, T. 4 S., R. 2 E., on the southeast side of Jackass Butte, Owyhee County, Idaho. This vole seems to be the most common species at this locality, judging by the recent collections made by Taylor and me.

Pliophenacomys parvus is distinguished from *P. meadensis* by its smaller size, slightly narrower molars with thinner enamel walls and by narrower re-entrant angles of the molars. The enamel is uniform in thickness. *Pliophenacomys parvus* is more advanced than *P. meadensis*, as shown by the loss of enamel on the anterior loop of M_1. The dentine on the anterolabial side of the anterior loop extends well above the base of the anterior re-entrant angle. With wear the anterior loop of M_1 in *P. parvus* presents an interrupted enamel pattern before the tooth is worn down to the base of the crown (Figs. 4 *J–K*). In *P. meadensis* there is no encroachment of the dentine on the anterior loop of M_1. The enamel extends downward to a level with the bases of the anterior re-entrant angles.

Among the specimens recovered of *Pliophenacomys parvus* is part of a left lower jaw, No. 21877 USNM, with the incisor, M_1 and

M_2 (Fig. 4*J*). The occlusal length of M_1 and M_2 is 4.75 mm. In the group of isolated teeth there are six first lower molars. They range in occlusal length from 2.5 to 2.8 mm., with an average of 2.6 mm. Root development in the molars is larger on *P. meadensis* than on *P. parvus*. M^1 is three-rooted with the inner root greatly reduced. M^2 and M^3 are two-rooted.

No cement is present on the molars of *Pliophenacomys parvus*. Its absence cannot be due to accidents of preservation, for the associated teeth of *Synaptomys* and *Ondatra* retain cement in the re-entrant angles of the molars.

Associated forms.—Directly associated with *Pliophenacomys parvus* were *Synaptomys vetus* Wilson and *Ondatra idahoensis* Wilson. In the immediate vicinity of this site (about fifty feet west and within five feet stratigraphically) I collected two larger mammals. A partial horse dentition represents a large zebra, tentatively identified as *Plesippus idahoensis* (Merriam). Part of a large antler is identified as *Cervus* cf. *lucasi* Hay.

Discussion.—I have examined isolated teeth of *Pliomys episcopalis bolkayi* Kormos from Podumci, Dalmatia, Yugoslavia, which were identified as *Dolomys episcopalis bolkayi* Kormos by Dr. Kowalski. The specimens were taken from deposits of Mindel age. The subspecies *bolkayi* is said to differ only from *Pliomys e. episcopalis* in its slightly larger size and higher crowned teeth.

In comparison with *Pliophenacomys parvus* the teeth of *P. e. bolkayi* are much higher crowned; root development occurs only in adult and old adult specimens (Fig. 4*N*). No cement is present in the re-entrant angles. The alternating triangles of the lower molars are more tightly closed than in *P. parvus* and especially the fifth alternating triangle of M_1, which is tightly closed off from the anterior loop in young adult specimens and remains so in old adult specimens. The fourth alternating triangle of M_2 is closed off from the third whereas in *Pliophenacomys* the third and fourth triangles of M_2 are confluent. The striking difference is the much higher crowned teeth of *P. e. bolkayi*, which have an advanced interrupted enamel pattern and have the enamel of the lower molars differentiated into thick and thin tracts as in the genus *Microtus*.

In young adult specimens of *P. e. bolkayi* the dentine tract on the anterolabial side of the anterior loop of M_1 extends upward 2.5 mm. above the base of the crown. There is a dentine tract the full length

of the labial edge of the posterior loop of M_1, but the dentine tract on the lingual edge of the posterior loop of M_1 lacks 1.0 mm. of reaching the occlusal surface. M_2 in young adult specimens has a dentine tract along the anterior face of the fourth alternating triangle where it joins M_1. This dentine tract in young specimens ends just short of the occlusal surface and with little wear produces an interrupted enamel pattern. There are both labial and lingual dentine tracts on the sides of the posterior loop. The labial tract is approximately three-fourths the crown length, and the lingual tract of dentine is two-thirds the crown length in young adult teeth. M_3 possesses the same dentine tracts as M_2. In these teeth the base of the crown has started to close, but roots have not developed. M_2 is decidedly curved labially as in *Microtus*, a marked contrast to the straight crowned M_2 of *Pliophenacomys parvus*.

An LM^1 of a young adult, specimen No. 34901 UMMP (Fig. 4 *L–M*), lacking roots and with a crown height of 4.0 mm., has a dentine tract along both the labial and lingual edges of the anterior loop which lacks 1.0 mm. of reaching the occlusal surface. The first lingual triangle has a longer dentine tract, which reaches within 0.5 mm. of the occlusal surface. A dentine tract extends the full length of the fourth or posterior triangle where it joins the anterior surface of M^2.

I consider *Pliomys episcopalis bolkayi* Kormos generically distinct from *Pliophenacomys parvus* because the teeth are much higher crowned, the roots of the teeth are greatly reduced, the occlusal pattern of the teeth have an advanced interrupted enamel pattern with differentiated enamel along the faces of the alternating triangles, and M_2 is strongly curved. *Pliomys episcopalis bolkayi* is the first of the rooted microtines I have studied that possesses characters that show some relationship to the genus *Microtus*. It is too young to be considered the ancestral stock, but it is probably closely related to the line that gave rise to the genus *Microtus*.

On account of the absence of cement in the re-entrant angles, I agree with Kretzoi that it is distinct from the recent *Dolomys bogdanovi* Martino, which possesses both an interrupted enamel pattern and cement in the re-entrant angles of the teeth. Kretzoi has placed the recent forms in the genus *Dinaromys*. I have examined teeth of *Dolomys dalmatinus* Kormos from Podumci, Dalmatia, Yugoslavia, of Mindel age, which were identified by Dr. Kowalski.

These specimens possess better developed roots than *Pliomys e. bolkayi*, but the teeth have an interrupted enamel pattern which is as advanced. Cement is present in the re-entrant angles of old adult teeth. I consider this form generically distinct from *Pliomys* and also from *Dolomys milleri* (Nehring), which lacks cement on the teeth. There is one question: does *D. milleri* possess an interrupted enamel pattern in adult and old adult specimens?

Since its true relationship to Eurasian forms is unknown, I have retained *Pliophenacomys parvus* Wilson tentatively in the genus *Pliophenacomys*, to which it is closely related.

Pliopotamys sp.

(Figs. 5 *A–B*)

A palate and isolated teeth of *Pliopotamys* were taken in association with the remains of *Pliophenacomys idahoensis* and other forms from USGS Locality 19128, Owyhee County, Idaho. They are the earliest record of *Pliopotamys* in North America.

Description of specimens recovered.—Four lower first molars show a posterior loop and five alternating triangles. The fifth triangle opens broadly into the anterior loop. Specimen No. 21827 USNM

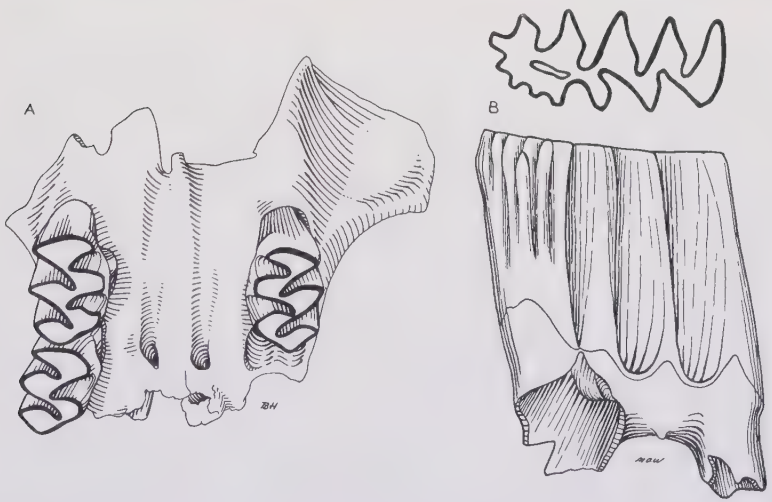

FIG. 5. *Pliopotamys* sp. *A*, USNM 21831, palatal view, × 4; *B*, USNM 21827, LM_1, labial and occlusal views, × 8.

(Fig. 5*B*) is a left M_1 of a young animal. Its occlusal length is 4.0 mm. In size it corresponds to *Pliopotamys minor*, but the reentrant angles are broader. The isolated first lower molars have longer roots than those of *P. minor*, with the same stage of wear. An M_1 of an old adult has an anteroposterior occlusal length of 4.15 mm.

Five upper first molars were found. Those of old adults possess larger roots than occur on M^1 of *Pliopotamys minor* from the Hagerman local fauna. The largest M^1 has an anteroposterior occlusal length of 3.2 mm. and a transverse width of 2.5 mm.

A single M^3 was found. It consists of an anterior loop, three alternating triangles, and a posterior loop, which is broken. The two anterior roots are fused, a condition not observed in *Pliopotamys minor* or *P. meadensis*.

The palate, No. 21831 USNM, is broken just posterior to M^2 (Fig. 5*A*). It contains the right and left upper first molars and RM^2. The occlusal length of M^1 and M^2 is 6.75 mm. The occlusal length of M^1 is 3.5 mm. and the width is 2.5 mm. The occlusal patterns of M^1 and M^2 are like those of *Pliopotamys minor*. The lingual side of the first alternating triangle of M^1 is flat. Better material is needed for definite specific assignment of the specimens.

Pliopotamys minor (Wilson)

(Figs. 6 *A–F*)

Ondatra idahoensis minor Wilson, 1933, Carnegie Inst. Wash. Publ., No. 440: 135.
Dolomys minor (Wilson) *non* Hibbard; Kretzoi, 1955, Acta Geol., 3(4): 348–355.
Pliopotamys idahoensis (Wilson), Hibbard, 1956, Pap. Mich. Acad. Sci., Arts, and Letters, 41 (1956): 176.
Pliopotamys idahoensis (Wilson) Hibbard, in Flint, 1957. Glacial and Pleistocene Geology, Wiley and Sons, p. 461.

The holotype of *Pliopotamys minor* is from the Hagerman formation and was recovered in the vicinity of the horse quarry (N. ½ NW. ¼ Sec. 16, T. 7 S., R. 13 E., Twin Falls County, Idaho).

Specimens of this vole were recovered by Dwight W. Taylor and myself in the summers of 1955, 1956, and 1957 from the following three localities south of the horse quarry: USGS Cenozoic Localities 19216, 19217, and 20765. At these three localities parts of at least sixteen individuals were found, as shown by the number of left first lower molars recovered. Most of these teeth are in fragmentary

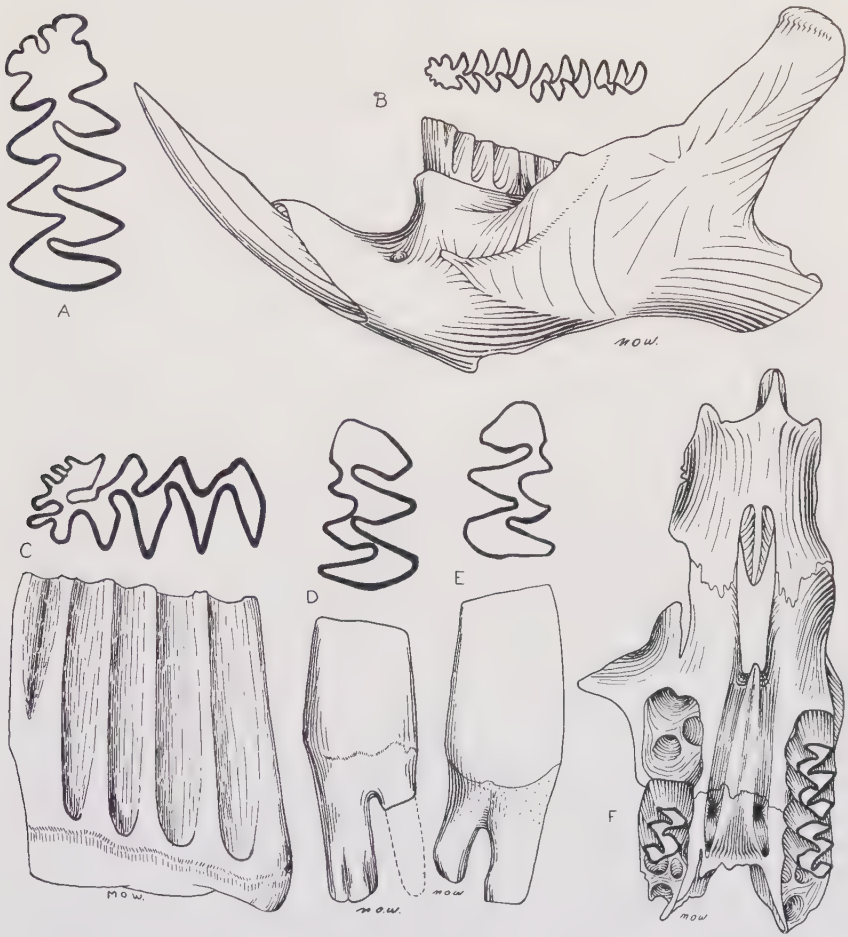

FIG. 6. *Pliopotamys minor*; *A*, USNM 21830, LM_1, occlusal view, × 8; *B*, UMMP 33895, left jaw, labial and occlusal views, × 3; *C*, UMMP 31421, right immature M_1, lingual and occlusal views, × 8; *D* and *E*, USNM 21829, left and right M^3, anterior and occlusal views, × 8; *F*, UMMP 33896, palatal view, RM^2, LM^1 and M^2, × 3.

jaws. Fragments of maxillaries were also found. No size differences were noted in the individuals from the different localities.

M_1 consists of a posterior loop and five alternating triangles, the fifth opening broadly into the anterior loop. The anterior loop is

decidedly crenulate in young specimens (Figs. 6 *A* and *C*). M_2 consists of a posterior loop and four alternating triangles, the third and fourth confluent. M_3 consists of a posterior loop, two alternating triangles, and an anterior loop. The second triangle is considerably smaller than the first. In *Ondatra* the labial triangles are not so small in comparison with the lingual triangles as they are in *Pliopotamys*. The lower molars are two-rooted. In old adult specimens a slight depression occurs labial to M_3, although it is not so pronounced as in adult specimens of *Ondatra*. A deep, broad groove separates the base of M_3 from the angle of the jaw. The condyle of the lower jaw curves slightly lingually but is not so pronounced as in *Ondatra*. There is a slight swelling on the labial side of the jaw which indicates the posterior position of the incisor. The incisor ends just above the upper edge of the dental foramen. Two nearly complete lower jaws found represent young adult individuals. The anteroposterior occlusal length of M_1–M_3 of specimen No. 33895, UMMP, is 9.8 mm. (Fig. 6*B*). The greatest occlusal lengths of M_1, M_2, and M_3 are 4.5, 2.7, and 2.5 mm. The anteroposterior occlusal length of M_1–M_3 of specimen No. 21829 USNM is 9.1 mm. The greatest occlusal lengths of M_1, M_2, and M_3 are 4.1, 2.5, and 2.5 mm. The anteroposterior occlusal length of eighteen other lower first molars measured varies from 4.0 to 4.8 mm., with an average length of 4.21 mm.; molars of four young individuals measured 4.0 mm. The greatest occlusal length of M_1 was 4.8 mm. in an old adult. The narrowest occlusal width of M_1 was 1.8 mm. and the greatest 2.0 mm.

A number of isolated teeth were recovered. All upper molars had three well-developed roots (Figs. 6 *D–E*). Cement is lacking on lower and upper molars.

A nearly complete palate and diastemal region of an adult (No. 33896 UMMP) contains a right M^2, left M^1 and M^2, and alveoli of the other missing teeth (Fig. 6*F*). The length from the posterior border of the alveolus of the incisor to the posterior border of the alveoli of M_3 is 22.4 mm. The diastemal length is 12.3 mm. The anterior palatine foramina are 7.4 mm. long. The lateral palatal grooves extend posteriorly from each of the foramen and end in a posterior palatal foramen opposite the anterior loop of M^2. The posterior edge of the palatine is nearly square and lacks a median posterior process. Posterior palatal pits are lacking. Posterior foramina are present. The lingual border of the maxillary forming

the labial border of the palatal groove is not deflected labially until it passes the anterior roots of M^3 (Fig. 6*F*).

Remarks.—Pliopotamys minor (Wilson) is distinguished from *P. meadensis* by the occlusal pattern of M_1. All occlusal patterns of M_1 in *P. minor* except that of one tooth have the fifth alternating triangle opening broadly into the anterior loop (see fig. 8*a*, Wilson, 1933). In the occlusal pattern of *P. meadensis* the apex of the third labial re-entrant angle is opposite or nearly opposite the apex of the fourth inner re-entrant angle (see fig. 5*A*, Hibbard, 1956). In all of the young and adult specimens of *P. meadensis* only one pattern was found like that of *P. minor* (see pl. I, fig. 6, Hibbard, 1938). Considerable variation occurs in the occlusal patterns of old adult specimens as the tooth is worn to the base of the crown.

The genus *Pliopotamys* is distinguished from the genus *Dolomys* Nehring (genotype, *Dolomys milleri* Nehring), by the presence of three well-developed roots on M^1, M^2, and M^3. *Dolomys milleri* has the third root of M^1 more reduced than in *Pliopotamys*, and M^2 and M^3 are two-rooted (Nehring, 1898; Méhely, 1914; and Hinton, 1926).

Kretzoi (1955) considered *Ondatra idahoensis idahoensis* Wilson and *Ondatra idahoensis minor* Wilson as belonging to the genus *Dolomys*. Kretzoi assumed, as I did (Hibbard, 1956, p. 176), that the two microtines described by Wilson from the Pleistocene of Idaho belong to the same genus. Although *Ondatra idahoensis idahoensis* Wilson is a true muskrat (*Ondatra*), I believe Wilson's other form is generically distinct, i.e., *Pliopotamys minor* (Wilson).

Ondatra idahoensis Wilson

(Figs. 7 *C–D*, *F–G*)

Ondatra idahoensis idahoensis Wilson, 1933, Carnegie Inst. Wash. Publ., No. 440, p. 132.

Only one isolated tooth of this species was found at the rodent site of the Grand View local fauna, Jackass Butte, USGS Cenozoic Locality 20764, Idaho. The following discussion is based principally on the original material in the California Institute of Technology collections.

A good description of this muskrat is given by Wilson (1933). The following comments concern the development of the dentine tracts along the sides of the teeth and the development of the inter-

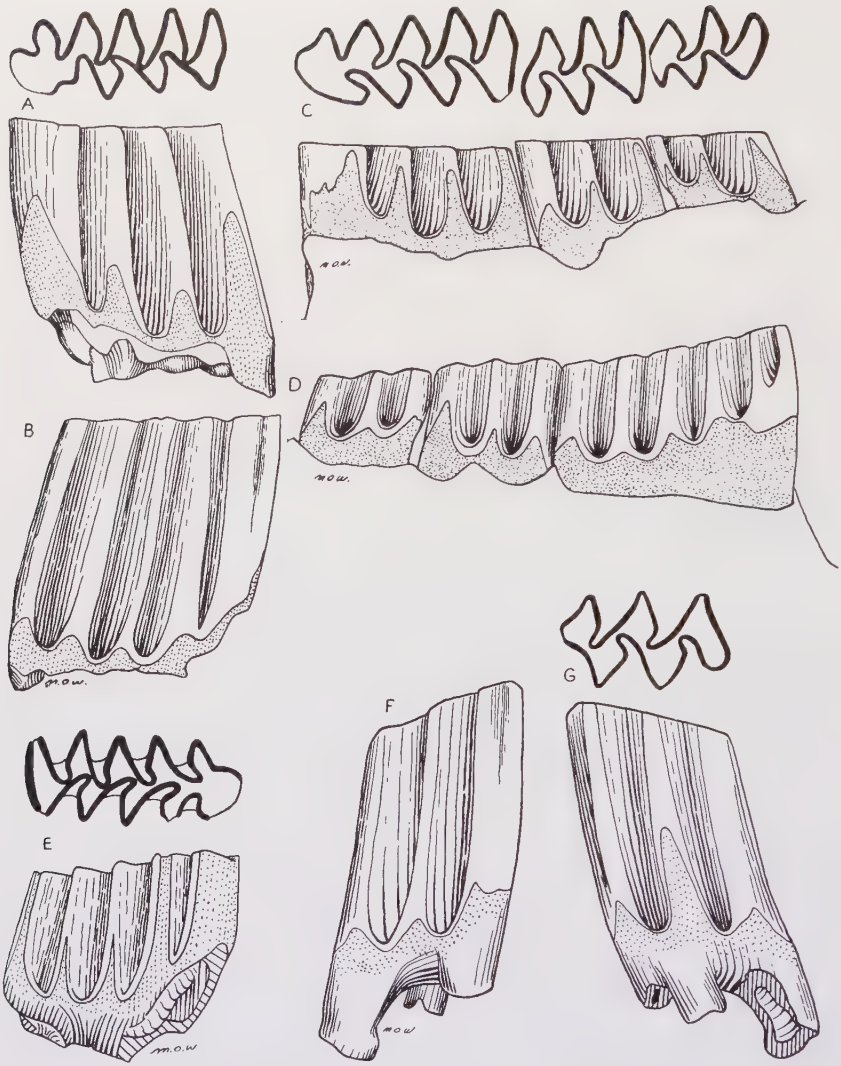

FIG. 7. *Ondatra*; *A* and *B*, *Ondatra* sp.; UMMP 32046, LM_1; *A*, labial and occlusal views; *B*, lingual view. *C* and *D*, CIT 1376, holotype, *Ondatra idahoensis*; *C*, left M_1–M_3, labial and occlusal views; *D*, left M_1–M_3, lingual view. *E*, *Ondatra kansasensis*, KUMNH 6662, RM_1, labial and occlusal views. *F* and *G*, *Ondatra idahoensis*, CIT 1377, RM^1; F, labial view; *G*, lingual and occlusal views. *A*–*D*, *F* and *G*, × 6; *E*, × 5.

rupted enamel pattern. The holotype, No. 1376, CIT is part of a left lower jaw of an adult muskrat bearing M_1–M_3. The antero-posterior occlusal length of the molar series is 10.1 mm. Interstitial cement is poorly developed in the re-entrant angles and occurs in the base of the labial anterior re-entrant angles of M_1. It is better developed in the lingual re-entrant angles of this tooth, especially at the base and along the sides of the angles, but not so well developed in the deep apex. Cement has not been deposited on the teeth of young specimens, but the dentine tracts are present along the sides of the teeth. Cement occurs on teeth of adult and old adult specimens. The dentine tracts are best developed on the labial side of the lower molars and the lingual side of the upper molars (Figs. 7 *C* and *G*). In the holotype the occlusal surface has worn down so that there is an interrupted enamel pattern on the labial side of the posterior loop of M_1 (Fig. 7*C*). With further wear the anterior loop would have had the enamel interrupted by the dentine. The enamel of M_2 and M_3 would have been first interrupted by the dentine tracts on the labial side of the posterior loops.

Discussion.—The dentine tracts on the sides of the teeth of *Ondatra idahoensis* do not appear to be as well developed as those of *O. hiatidens* (Cope) (see Hibbard, 1955) or of *O. kansasensis* Hibbard (Fig. 7*E*). There is evidence, however, that some individuals or species of *Ondatra* did not have as well-developed dentine tracts as others. I (1956, p. 177) referred a left lower molar, No. 32046 UMMP, of a young individual from the Borchers local fauna to *Pliopotamys* because of its lack of cement. After comparison of this tooth (Figs. 7 *A–B*) with the series from the Grand View local fauna, I find that the tooth is that of an immature *Ondatra*, in which the roots or cement were not developed. As is visible in Figure 7*B*, the dentine tracts are developed on the lingual side as they are in *O. idahoensis*. This may be due to the lack of a well-defined crown and roots. No tooth of comparable age wear is known from the Grand View local fauna which can be used for comparison. The dentine tracts are not as well developed as in *O. kansasensis* of the Kansan age Cudahy fauna of the High Plains. It may well be that some of the early species of *Ondatra* were more progressive in the development of higher dentine tracts along the sides of the teeth than were others. The deposition of cement may also be an age character that varies in early *Ondatra* species.

MAMMALIA

Hypolagus furlongi Gazin, 1934
Castor cf. *accessor* Hay, 1927
Synaptomys vetus Wilson, 1933
Ondatra idahoensis Wilson, 1933
Pliophenacomys parvus (Wilson) 1933
Erethizon bathygnathum Wilson, 1935
Felis cf. *lacustris* Gazin, 1933
Lutra (*Satherium*) *ingens* Gazin, 1934
Plesippus idahoensis (Merriam), 1918
Cervus cf. *lucasi* Hay, 1927

Grand View local fauna.—In this discussion I have summarized the Grand View local fauna and reconsidered its age and environmental interpretation. This section is based partly on newly available material and partly on re-evaluation of older information.

The location indicated by Wilson (1933, p. 120) is identifiable as Jackass Butte, Jackass Butte quadrangle, in spite of the lack of precise locality description. N. R. Anderson, College of Puget Sound, Tacoma, Washington, corresponded with Wilson and also attempted to examine the field notebooks of the California Institute of Technology party which originally collected at the Grand View site. The field data could not be found, but Wilson sent what information he recalled to Anderson. The CIT material came primarily from the southern and eastern sides of Jackass Butte, but some is from beds directly across the river. All of the rodent specimens came from a single bed.

This information was the basis for field examination of the area by Anderson and Taylor, and later by Taylor and Hibbard. At least at Jackass Butte, only one sedimentary unit is involved—a series of olive clay interbedded with lighter silt and fine sand. The fine grain size and lenticular bedding suggest deposition by a slow-moving stream aggrading its flood plain. In grain size, color, and bedding, this sequence is strikingly similar to the type Hagerman formation. Certainly most, and probably all, of the original CIT material came from this unit. The later collection of *Ondatra*, *Pliophenacomys*, and *Synaptomys* at USGS Locality 20764 strongly suggests that this is the type locality for the three species described by Wilson. The horse material described by Schultz (1936) apparently came from both Jackass Butte (CIT Locality 119) and north of the Snake River opposite Jackass Butte (CIT Locality 118).

The inferences from the fauna as a whole can be divided into the

types of evidence that suggest the Grand View local fauna is (a) younger than the Hagerman local fauna; (b) of interglacial rather than glacial age; and (c) most probably of Yarmouth age. The detailed consideration of each species follows the more general discussion.

1. Relationship of the Hagerman and Grand View local faunas. All of the paleontologists who have considered the relative age of the Hagerman and Grand View local faunas have concluded that the Grand View local fauna is younger (Wilson, 1937b; Gazin, 1934b, p. 119; 1936, p. 286). This belief, further maintained here, is based on the small percentage of mammals common to the two faunas, on the inferred structural progressiveness of related species in the Grand View local fauna, and on correlation of these two faunas with assemblages in the Great Plains where an age difference is demonstrable.

The mammals of the Hagerman local fauna were listed by Gazin (1936). Comparison of that Hagerman list with the summary of the Grand View assemblage given above shows there are only two species which may be common to both faunas: *Felis lacustris* Gazin and *Castor* cf. *accessor* Hay. The former is a puma-like cat of relatively long geologic range. It is not significant for discrimination of the small time segments concerned here. The beaver *Castor* from the Hagerman local fauna has never been studied in detail, and the necessary careful comparisons between the Hagerman and Grand View material are not available. It is therefore not at all certain that the same species of beaver occurs in both assemblages. Stirton (1935, p. 446) referred to the Hagerman species as *Castor* cf. *californicus* but did not discuss the relationship of *C. accessor* Hay.

A second line of reasoning that suggests that the Grand View local fauna is younger than the Hagerman local fauna is the inferred structural progressiveness of Grand View species over their Hagerman relatives. The following pairs of related species have the more advanced form in the Grand View local fauna, the less advanced one in the Hagerman local fauna.

Hagerman	Grand View
Pliopotamys minor (Wilson)	*Ondatra idahoensis* Wilson
Plesippus shoshonensis Gidley	*Plesippus idahoensis* (Merriam)
Lutra piscinaria Leidy?	*Lutra ingens* Gazin

A third kind of evidence for the younger age of the Grand View local fauna is the younger age of its correlatives compared to the Hagerman correlatives. The early Pleistocene age of the Hagerman local fauna is now rather generally accepted by vertebrate paleontologists. I (Hibbard in Flint, 1957; Hibbard, 1958c) have referred it to the Aftonian, but it may possibly be of Nebraskan age. Correlatives of the Hagerman local fauna which are of early Pleistocene date, but not necessarily from the same glacial or interglacial interval, are the Blanco local fauna of Texas; the Dixon, Deer Park, and Sanders local faunas of Kansas; and the Sand Draw local fauna of Nebraska. Evidence of the fossil mammals suggests that the Grand View local fauna is related not to these, but to distinctly younger assemblages. Relationships of three Grand View species are summarized below.

Synaptomys vetus Wilson: Nearest relative is in the Borchers local fauna, Kansas.

Ondatra idahoensis Wilson: Stage of development of this species is most like that of *Ondatra* of the Borchers local fauna.

Pliophenacomys parvus (Wilson): Nearest relative is in the Sanders local fauna, Kansas, but it is definitely more advanced than that species.

The Borchers local fauna is in a formation unconformably overlying that which has yielded the Deer Park and Sanders local faunas. These three assemblages are all in Meade County, Kansas, and their stratigraphic relations have been demonstrated (Hibbard 1949, 1956, 1958a).

2. Interglacial age of Grand View local fauna. Evidence of the glacial or interglacial age of the Grand View local fauna must come at this time from comparison with the known assemblages of the Great Plains. Southern Idaho is the only area west of the Rocky Mountains where even the beginning of a varied sequence of Pleistocene nonglacial deposits is known. As such, it holds considerable promise for translating detailed late Cenozoic correlations toward the Pacific Coast.

Unfortunately the basis for believing the Grand View local fauna to be of interglacial age is largely negative evidence. It consists of the absence of such small mammals as *Synaptomys* (*Mictomys*) *borealis* (Richardson), *Microtus*, and *Sorex*. These are forms of northern distribution in the United States today that characterize post-Nebraskan glacial faunas of the southern High Plains, in south-

western Kansas and western Oklahoma. If the Grand View fauna were of glacial age, one might expect such boreal elements.

A variety of mollusks is not yet known from the Grand View local fauna. When obtained, this will be of considerable help in interpreting the environment of the fauna.

3. Yarmouth age of Grand View local fauna. The evidence presented so far indicates that the Grand View local fauna is younger than the early Pleistocene Hagerman local fauna and is more probably of interglacial than glacial age. The weight of present evidence favors a Yarmouth age. The stage of evolution and the nearest relatives of *Synaptomys vetus*, *Ondatra idahoensis*, and *Pliophenacomys parvus* suggest correlation with the Borchers local fauna of southwestern Kansas. This assemblage is definitely interglacial, and if there were but three interglacial ages it is of Yarmouth age (Hibbard, 1949).

Age relationships of Grand View local fauna.—This section summarizes the age significance of each mammal in the fauna, on which the preceding discussion was based.

1. *Hypolagus furlongi* Gazin. Gazin (1934b) concluded that *H. furlongi* is closely related to the Hagerman species *H. limnetus*: "... probably the deposits in which remains of the two were found are of slightly different age as indicated by the specific differences observed between the otters and some of the rodents. In these cases the Grand View stage appears somewhat more advanced."

2. *Castor* cf. *accessor* Hay. Hay (1927, p. 266) described this beaver from material collected by N. F. Drake (see Lindgren, 1900, p. 99; Lindgren and Drake, 1904, pp. 2–3). The locality was given originally as "Two and one-half miles NNW. of ferry where Caldwell-Rockville road crosses Snake River; elevation 2,500 feet; collector, N. F. Drake; soft lake beds forming bluffs facing Snake River." The map published by Lindgren and Drake indicates this location is in or close to the N. ½ Sec. 7, T. 3 N., R. 4 W.; now in Canyon Co., Idaho.

Inadequacy of both the Grand View material and the type of *Castor accessor* prevents definite identification of the Grand View material (Wilson, 1933, pp. 123–124). Beaver material from the Hagerman local fauna has been listed as *Castor accessor*? Hay (Gazin, 1936, p. 285), and as *Castor* cf. *californicus* (Stirton, 1935, p. 446). Until the Hagerman material has been studied in detail, however,

the relationships of the Grand View and Hagerman beavers will remain uncertain. At this time the Grand View *Castor* has no precise age significance.

3. *Synaptomys vetus* Wilson. The closest relative of this species is *S. landesi* Hibbard, from the Borchers local fauna of Kansas.

4. *Ondatra idahoensis* Wilson. The earliest known occurrence of this genus is in the late Kansan Cudahy fauna of the Great Plains. It is not known from the Hagerman local fauna; nor from the late Nebraskan age, Sand Draw local fauna, Nebraska; nor from the transitional Nebraskan-Aftonian Dixon local fauna, Kansas; nor from the Aftonian Deer Park and Sanders local faunas of Kansas. All these assemblages have been reasonably well sampled, especially those in Kansas, so that these negative occurrences do carry some weight. The absence of this muskrat in the Hagerman local fauna is especially striking, for the type of sediments comprising the Hagerman formation and the general aspect of the fauna (Gazin, 1936, p. 285) strongly indicate that it would have found a congenial if not ideal habitat. The related *Pliopotamys* in the Hagerman fauna further supports such an inference. The suggestion is strong that *Ondatra* is absent from the Hagerman local fauna because it had not yet evolved, or had not yet immigrated into the Snake River Valley.

Compared to other Pleistocene muskrats, *Ondatra idahoensis* is closest in its stage of development to that from the Borchers local fauna of Kansas.

5. *Pliophenacomys parvus* (Wilson). This vole is most closely related to *P. meadensis* Hibbard, of the Aftonian Sanders local fauna, Kansas. It is, however, definitely more advanced than that species.

6. *Erethizon bathygnathum* Wilson. Porcupines are rare fossils, and hence it is not surprising this species lacks stratigraphic value. It may be the earliest record of the genus.

7. *Felis* cf. *lacustris* Gazin. This species was described from the Hagerman local fauna, and two specimens from the Grand View site referred to it. It does not possess great stratigraphic significance, partly because rather adaptable large cats of this type seem to be fairly long ranging.

8. *Lutra* (*Satherium*) *ingens* Gazin. The Grand View otter is distinct from the Hagerman species by the greater size and massiveness of its jaw. It may well be descended from the latter. Whether

L. ingens was a larger animal, or differed mostly in proportions, is uncertain.

Lutra piscinaria Leidy (1873, p. 316) is of uncertain relation to the Grand View and Hagerman species. It is based on a tibia from the indefinite locality Sinker Creek, Idaho, and comparable material from the Grand View local fauna is unknown. As indicated by Gazin (1934, p. 149) *L. piscinaria* may be the Grand View rather than the Hagerman form.

9. *Plesippus idahoensis* (Merriam). This species was described on the basis of material from two localities (Merriam, 1918, p. 527):

a) "near Froman Ferry on the Snake River, eight miles southwest of Caldwell, Idaho." The locality record at the University of California Museum of Paleontology lists Locality 3036 as two miles plus northwest of Froman Ferry, 7–8 miles southwest of Caldwell, Idaho, T. 3 N., R. 4 W., Sec. 7. Evidently two specimens (including the holotype) of this horse come from very close to, if not indeed from, the type locality of *Castor accessor* Hay.

b) "north bank of the Payette River, about four and one-half miles southeast of the town of Payette." UCMP Locality 3039. The locality record at the University of California Museum of Paleontology adds the information that this site is on Horn's ranch.

There is no independent evidence of the age of these two localities. The principal significance of this horse in the Grand View local fauna is that it is distinct from the Hagerman *Plesippus shoshonensis*. *P. idahoensis* is the youngest known species of the genus in North America. Schultz (1936) referred this species to *Plesippus*, although he recognized that there were *Equus*-like features in it.

10. *Cervus* cf. *lucasi* Hay. This elk was described from Sand Hollow, Ada County, Idaho, from an astragalus and phalanx (Hay, 1927, pp. 110–111). The two Grand View specimens are parts of antlers, and hence cannot be referred with any certainty to Hay's form. There is no independent evidence for the age of the original specimens of *C. lucasi*.

Correlative occurrences in Idaho.—So far, the Grand View local fauna is the only middle Pleistocene assemblage recognized in Idaho. There are several scattered occurrences (such as those in the Payette River valley) which may be correlative, but are indeterminate. The site near Froman Ferry is quite possibly of middle Pleistocene age

and correlative with the Grand View fauna, however. The evidence of *Plesippus idahoensis* and *Castor accessor* is suggestive, but not definitive.

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A NEW PLIOCENE CAT FROM KANSAS

JOHN J. STEPHENS
University of Michigan

The large Rexroad local fauna of Meade County, Kansas, contains an outstanding assemblage of vertebrates (Hibbard, 1950; Taylor, 1941; Wetmore, 1944). The new species described below is one of the short-faced cats related to *Felis lacustris* Gazin.

The holotype of *Felis lacustris* is known from the lower jaw (No. 12611, USNM), described by C. Lewis Gazin (1933), from the Hagerman local fauna, Hagerman formation, Twin Falls County, Idaho.

Felis rexroadensis, sp.nov.

(Fig. 1 *A–F*)

Holotype.—Upper jaws, brain case, right and left petrosal bones, UMMP 34195. Premaxillaries with incisors, maxillaries with P^3 and P^4 and alveoli for C and M^1. Paratypes: UMMP 29644, partial right maxillary with C, P^3 and P^4, partial left maxillary with C, P^3, P^4, and M^1; UMMP 34196 is a left upper jaw with complete maxillary and part of the frontal, and maxillary with P^3 and P^4.

Horizon and type locality.—Upper Pliocene, Rexroad formation, Rexroad fauna, University of Kansas, Meade County, Locality No. 3, W. ½, SW. ¼, Sec. 22, T. 33 N., R. 29 W., Rexroad Ranch, Meade County, Kansas.

Diagnosis.—A *Felis* smaller than *F. lacustris* Gazin. Differentiated from Recent cats in having a petrosal bone with expanded anterior border; from an undescribed petrosal of *F. lacustris* (UKMNH 4664) from the Rexroad local fauna, Locality 2A, in being smaller and having a more complicated surface. The form differs from *F. peii* Chardin (1945), of which the petrosal is unknown, in having a narrower palatal width across the distal extremities of the P^4.

Description.—P^2 is greatly reduced in the younger specimen (Fig. 1*D*) and is completely lost in the adult with the closure of the alveolus taking place (Fig. 1*A*). The P^3 is compressed laterally in comparison with *Felis lacustris*; P^4 bears a rather deep carnassial

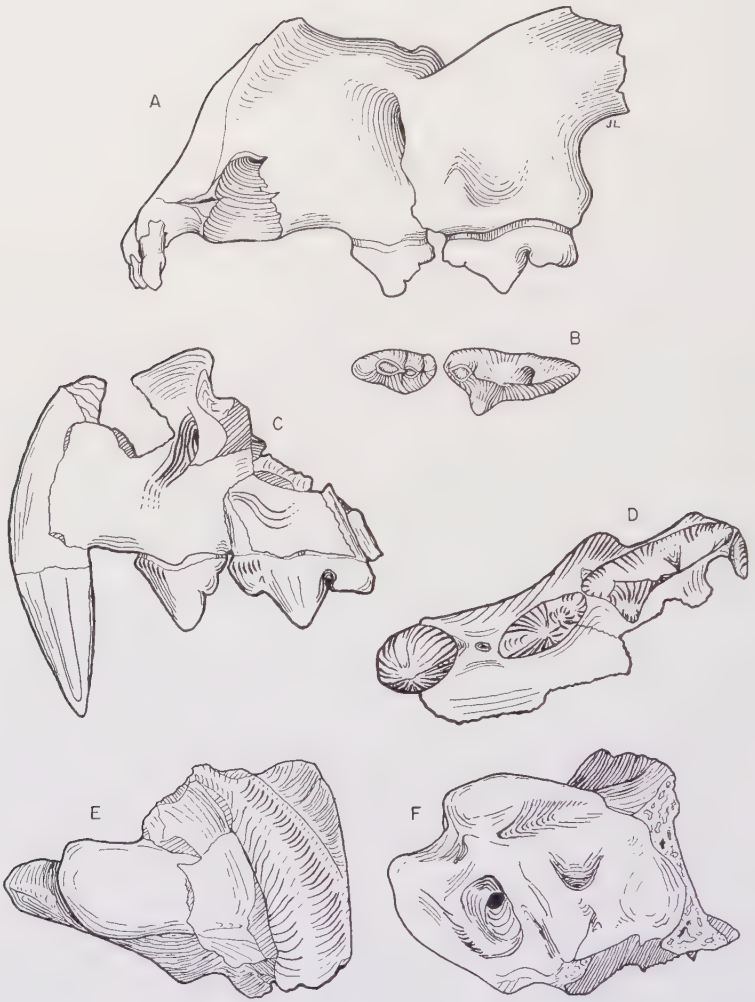

FIG. 1. *Felis rexroadensis: A*, UMMP 34195, part of left upper jaw, I^1–I^3, P^3–P^4, lateral view; *B*, UMMP 34195, P^3–P^4, occlusal view; *C*, UMMP 29644, part of left upper jaw, C–M^1, lateral view; *D*, UMMP 29644, palatal view; *E-F*, UMMP 34195, right petrosal bone, dorsal and internal lateral view. *A–D*, × 1; *E–F*, × 2.

notch. The diastema between I^3 and the canine is 6.1 mm. I^1 and I^2 are approximately the same size, but I^3 is larger and expanded at the upper enamel edge (Fig. 1*A*). The incisors lie in a nearly straight row. The greatest occlusal width of the incisors is 6.8 mm.

The palatal pits are situated just medially of the posterior part of the P^4 and are deeper than those found in Recent cats of the same size. The anterior palatine foramina parallel the midline, whereas in *Lynx rufus* Schreber, they open posteriorly at an angle to the midline.

The greatest height of the premaxillary, measured from the border of the alveolus for the canine to the dorsal border of the ascending ramus, is 30.5 mm.; the greatest transverse width from the midline to the anterior border of the alveolus of the canine is 13.3 mm.; the depth at the symphysis is 8.5 mm.; and the greatest anteroposterior length measured at the midline is 12.1 mm.

The greatest anteroposterior length of the maxillary measured from the anterior suture to the posterior edge of the alveolus for the M^1 is 48.7 mm.; the greatest height from the anterior edge of P^3 to the most dorsal extremity is approximately 44.4 mm. (measurement taken on crushed specimen, UMMP 34196); the greatest anteroposterior length from the posterior border of the premaxillary to the anterior border of the lachrymal foramen is 22.7 mm. The palatal width measured from the external surface opposite the alveolus of the first upper molars is approximately 57.6 mm.

The brain case is slightly wider than that of *Lynx rufus*. It has the following measurements; greatest anteroposterior length at midline, 75.2 mm.; greatest transverse width slightly anterior to auditory region, 55.0 mm.; greatest height in the auditory region, 47.0 mm.; and greatest width of the anterior end, 37.2 mm.

The petrosal bears an expanded and heavy anterior border (Fig. 1 *E–F*) that is not found in any of the Recent cats available for study. The anteroposterior length of the petrosal is 17.8 mm.; the dorsoventral height is 10.2 mm.; and the greatest transverse width is 13.3 mm. The consistent difference observed in the petrosal in the various specimens of Recent cats studied indicate that the features of this bone can be used in distinguishing the different species of cats.

Description of paratypes.—Specimen No. 29644 is a young adult (Fig. 1 *C–D*). The cusps of the teeth are slightly worn. The upper second premolars are missing, and the alveoli are greatly reduced. M^1 is intermediate in size in comparison with the M^1 of *Felis lacustris* Gazin and *Lynx rufus* Schreber. The greatest anteroposterior length of M^1 is 3.1 mm., and the greatest transverse width is 6.9 mm., compared with 3.7 mm. and 7.8 mm., respectively, in *F. lacustris*

(USNM 13743). The canine is ridged and bears a flattened lingual surface. In *F. lacustris* the canine is larger and more rounded on the lingual surface.

Specimen No. 34196, although crushed, was of use in determining an approximate size of the maxillary and the size of the P^3 and P^4. The measurements of the teeth in the three specimens discussed, and those of *Felis lacustris*, are listed in Table I.

Comparison with other species.—Felis rexroadensis is smaller than *F. lacustris* Gazin and *F. concolor* Linnaeus. It is slightly larger than *Lynx canadensis* Kerr and may be distinguished from it by the presence of the P^2 in the younger form (No. 29644). P^2 is reduced and, from material at hand, it appears to be shed early in life. The alveoli are closed in the older form (No. 34195). Further distinction is made on the basis of the petrosal, which possesses a massive anterior border appreciably larger than that found in *Felis concolor* Linnaeus, *F. pardinoides* Thomas, *F. wiedii* Goldman, *F. yagouaroundi* True, *F. pardalis* Linnaeus, *Lynx rufus* Schreber, *L. canadensis* Kerr, and many other cats.

TABLE I

Measurements of the Teeth of *Felis rexroadensis* and *F. lacustris*

	F. rexroadensis			*F. lacustris*
	No. 29644 mm.	No. 34195 mm.	No. 34196 mm.	No. 13743 mm.
Length of diastema, C-P^3	5.8	8.1	....	8.0*
Length from anterior border of P^3 to posterior border of P^4	32.3	29.9	31.4*	36.0*
C, length of crown measured from upper edge of enamel	21.0	....	....	25.8
C, greatest anteroposterior length at upper edge of enamel	9.8	....	....	11.9
C, greatest transverse width at upper edge of enamel	7.4	....	....	9.6
P^3, greatest anteroposterior length	12.6	11.2	12.3	13.7
P^3, greatest transverse width	7.0	5.5	5.6*	8.6
P^4, greatest anteroposterior length	19.2	17.9	18.7	22.1
P^4, greatest transverse width	9.5	8.7	7.6*	10.1

* Approximated measurements in millimeters.

Felis proterolyncis Savage from the Optima local fauna (Hemphillian) of Oklahoma (Savage, 1941) is smaller than *Lynx rufus* and on this basis would be much smaller than the described species. *Felis longignatus* Shotwell from the McKay Reservoir local fauna (Hemphillian) of Oregon (Shotwell, 1956) is larger than *L. rufus* and *F. proterolyncis*, but from the information given by Shotwell it appears to be smaller than *L. canadensis*. As stated before *F. rexroadensis* is larger than *L. canadensis*. The above fossil forms are known only from lower jaws. It is therefore impossible to make direct comparison with the upper jaw material. A series of measurements of the dentition from associated upper and lower jaws of *F. concolor* and *L. canadensis* were made. It has been found that the measurements made on the lower jaw from the posterior border of the canine to the posterior border of the M^1, compared to the measurements on the upper jaw from the posterior border of the canine to the posterior border of the P^4, is .22 times larger in both sexes of the two species. On the basis of these measurements it is assumed that *F. rexroadensis* would have had a lower dentition length, as taken above, that would range from 45.8 mm. to 47.9 mm. If the upper and lower dentitions of *F. rexroadensis* had the same ratio as the Recent cats studied, it definitely would be larger than *F. longignatus* Shotwell.

A comparison of the size of P^3 and P^4 in *Felis concolor*, *Lynx rufus*, and *L. canadensis* shows that the male teeth are 1.15 times larger than those of the female. The difference between the described species and *F. lacustris* is 2.2 times. It seems conclusive that the new species is not *F. lacustris*.

Acknowledgments

Through the kindness of Dr. C. Lewis Gazin, I report on the maxillary with teeth (USNM 13743) collected by G. B. Pearce in 1934, one mile south of the *Plesippus* quarry. The cat is a part of the Hagerman local fauna of Idaho (Gazin, 1936).

My thanks are due H. M. Van Deusen, American Museum of Natural History, Peter P. Vaughn, University of Kansas Museum of Natural History, and W. H. Burt, University of Michigan Museum of Zoology, for making available for study specimens of recent and fossil forms. I am indebted to Claude W. Hibbard, Curator of Vertebrate Paleontology, University of Michigan Museum of Paleon-

tology, for permission to describe the specimens collected by him. Figures 1*A* and *B* were drawn by Jean Libby Eggleton (J. L.).

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A FOSSIL ALLIGATOR FROM THE LOWER PLIOCENE OF OKLAHOMA AND ITS CLIMATIC SIGNIFICANCE

MICHAEL O. WOODBURNE
University of Michigan

Remains of alligators have been found in beds of Pliocene age in Nebraska and Oklahoma during the past few decades (Fig. 1). This would seem to tie in with the generally accepted idea of a warm, humid climate during part of the Pliocene.

In 1951 alligator dermal plates and skull fragments were taken from the Laverne formation, Lower Pliocene. There are two localities, one six miles south of Gate, Oklahoma, near the center of Sec. 5, T. 3 N., R. 28 E.C.M., and the other on the Barth Ranch near the center of the W. ½, Sec. 15, T. 1 N., R. 28 E.C.M.

The most recognizable fragment, UMMP 29145 (Pl. 1, Fig. 3), was found at the first locality. It is an incomplete squamosal bone 93 mm. long and is comparable in size to a complete squamosal bone (Pl. 1, Fig. 4), whose greatest length is 131 mm. from an alligator approximately nine feet long. Of the two more complete dermal plates, UMMP 34867 (Pl. 1, Fig. 2) was found at the locality south of Gate, a short distance from the squamosal bone. The other plate, UMMP 31825 (Pl. 1, Fig. 1) was discovered at the Barth Ranch locality. Both of these localities are represented by the open circle on the map in Figure 1.

Other Pliocene alligators have been found in Nebraska and Oklahoma. Mook (1946) found an alligator in the upper Ash Hollow, Middle Pliocene, on the George Sawyer Ranch in the S.E. ¼, Sec. 5, T. 31 N., R. 30 W., Cherry County, in northwestern Nebraska.

Savage (1941) lists an alligator from the Optima fauna, Middle Pliocene, near Optima, in Texas County, Oklahoma.

The present-day distribution of alligators is contained within the Coastal Plain (Fig. 1) and falls inside of the Austroriparian Biotic Province as defined by Dice (1943). It is of generally low topography, and the streams are sluggish for the most part. Swamps and marshes are prevalent in the low areas, and there is enough rainfall to support hardwood forests. The summers are hot and humid

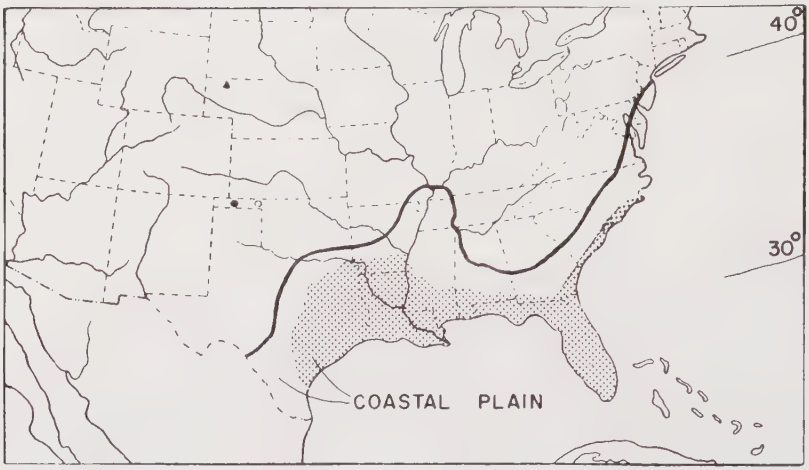
40°
30°
COASTAL PLAIN
Open symbol is Lower Pliocene
Closed symbols are Middle Pliocene
Stippled area is the present distribution of alligators in the U.S.

Fig. 1. Map showing the fossil localities and the present distribution of *Alligator mississippiensis* in the United States.

with an average temperature from 80° to 85°F. (Visher, 1954); the winters are mostly mild, with an average temperature between 45° and 55°, with highs of 65° in southern Florida. The annual precipitation is, on an average, fifty inches and falls mostly in the summer. The winter is mainly dry. Vegetation is especially abundant along the streams and in the lower swampy areas.

The mode of nesting of alligators seems to be dependent on these conditions of rain during the hot summers and abundance of vegetation. Persons who have studied this (McIlhenny, 1934, Reese, 1915, and Kellogg, 1929) seem to agree that large (about seven feet by three feet) nests are built of the most readily available vegetation in the area and are packed by being crawled over. The eggs are laid in a hole in the center. The nest serves as an insulator against the changing external temperatures while generating heat of its own through the decaying of the vegetable matter. This heat seems the most essential in incubating and hatching the eggs, and also the nest must be kept moist either by rain or micturition.

With favorable conditions hatching takes from sixty to seventy

days. McIlhenny, however, describes what he calls an "unusual" nest made of dry leaves on top of which dry earth was scraped. The nest was kept moist as usual, but the eggs took much longer to develop because of the absence of heat from decaying vegetable matter.

The area containing the fossil localities falls mainly in Dice's Kansas Biotic Province, which is higher and less humid than the coastal plain. The summers are hot, the temperature normally averaging between 70° and 75°. The evaporation rate is high because of the fairly constant winds. The vegetation is mostly grasses and sagebrush, although cottonwood trees and marsh vegetation are found where there is water. The amount of annual precipitation is small, about eighteen inches.

The present climate in the area is markedly different from what it must have been during much of the Pliocene. The Pliocene flora found in Beaver County, Oklahoma, indicates a more mild, uniform and moist climate than that at present (Chaney and Elias, 1936). The nesting habits of alligators require vegetation, which in turn requires the climatic conditions to produce it. The presence of alligators as far north as northwestern Nebraska in the Middle Pliocene would also indicate a more mild and moist climate than is found there now. There would at least have to be large, sluggish rivers with associated vegetation. These points are in agreement with the idea of a warm, mild climate for the earlier parts of the Pliocene. References to the Lower Pliocene vertebrate and molluscan faunas of the Laverne formation are given in Hibbard, 1951, and Taylor, 1954a and 1954b.

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PLATE 1

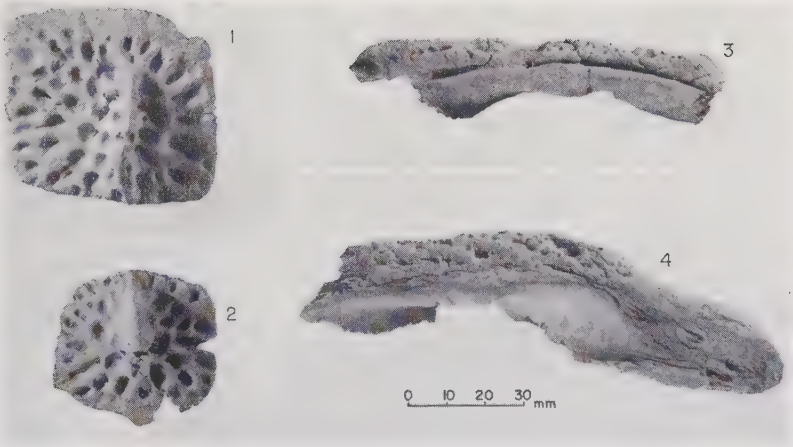

FIG. 1. Dermal plate *Alligator* sp., UMMP 31825.
FIG. 2. Dermal plate *Alligator* sp., UMMP 34867.
FIG. 3. Squamosal bone *Alligator* sp., UMMP 29145.
FIG. 4. Squamosal bone *Alligator mississippiensis*.

ZOOLOGY

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THE AMERICAN SPECIES OF THE GENUS *TETANOCERA* DUMÉRIL (DIPTERA)

GEORGE C. STEYSKAL
Grosse Ile, Michigan

The genus *Tetanocera* is one of the dominant and typical genera of the family Sciomyzidae, long known commonly as swale-flies, since most of them are found in swales, marshes, and similar wet localities. Berg (1953) has recently shown that probably all species of the family are parasitic or predaceous upon snails.[1]

Species of *Tetanocera* are found throughout the Holarctic region. Twenty-five species are known from the Palaearctic region. Five of these and twenty-two others are here listed from the Nearctic region as far south as Mexico City, a total of twenty-seven. The species are most abundant in the north; several have been found within the Arctic Circle.

The genus may be separated from other members of the subfamily Tetanocerinae by the following characters:

Vallar bristles absent.
Ocellar bristles well developed.
Hind tibiae with one dorsal preapical bristle.
Two fronto-orbital bristles present.
Arista with well-developed black or blackish hairs.
Second antennal segment at least one third, usually more than half, as long as third, tapered.
Mesopleura and pteropleura bare.
Sternopleura lacking distinct bristles, with hairs only.
Postabdomen of male with anal orifice well removed dorsad from surstyli.

The genus closest to *Tetanocera* is apparently *Renocera*. The only characters available at present to distinguish all species of *Renocera* from *Tetanocera* is the short, second antennal segment of the former, which is less than one-third as long as the third segment. Preliminary work on *Renocera*, however, shows that although it is a rather

[1] Berg, C. O., 1953. Sciomyzid larvae (Diptera) that feed on snails. Jour. Parasit., 39: 630–636.

heterogeneous assemblage, the various species are all quite distinct from *Tetanocera*. The Palaearctic genus *Chasmacryptum* Becker may be very close to *Tetanocera*. A few Central and South American forms, including the genus *Tetanoceroides*, are also related, and the New Zealand genus *Eulimnia* Tonnoir and Malloch may also have affinities to *Tetanocera*.

Genus *Tetanocera* Duméril[2]

1800 (Nov. 21–Dec. 20), Jour. Phys. Chim. Hist. Nat. Arts (Paris), 51: 439; Loew, 1847, Stettiner Ent. Ztg., 8: 250; Loew, 1862, Monogr. Dipt. No. Am., 1: 108; Van der Wulp, 1897, Biol. Centr. Am., Dipt., 2: 357; Osten Sacken, 1900, Verhandl. Zool.-Bot. Ges. Wien, 1900: 450; Hendel, 1900, *op. cit.*: 319; Hendel, 1903, Zts. Hym. Dipt., 1: 35; Aldrich, 1905, Smithsonian Misc. Coll., 46 (Cat. No. Am. Dipt.): 579; Coquillett, 1910, Proc. U.S. Nat. Mus., 37: 588; Hendel, 1910, Wien. Ent. Ztg., 29: 307; Melander, 1920, Ann. Ent. Soc. Am., 13: 326; Hendel, 1923, Konowia, 2: 209; Frey, 1924, Notulae Ent., 4: 47; Séguy, 1934, Faune de France, 28: 276; Curran, 1934, Fam. Gen. No. Am. Dipt.: 369; Sack, 1939, in Lindner, Die Fliegen d. pal. Reg., 5, fasc. 37: 48; Verbeke, 1948, Bull. Mus. Roy. Hist. Nat. Belg., 24: 19; Sabrosky, 1951, Ann. Ent. Soc. Am., 44: 566; Mayer, 1953, Ann. Naturhist. Mus. Wien., 59: 205.

Mycetomyza Fallén, 1810, Spec. Ent. Nov. Dipt. Disp. Meth. Exh.

Chaetomacera Cresson, 1920, Trans. Am. Ent. Soc., 46: 54.

Chaetotelanocera (*sic*; as subgenus) Mayer, 1953, Ann. Naturhist. Mus. Wien, 59: 206.

This list is not complete; most of the older European references have been omitted.

There is relatively little diversity in the genus, even the male postabdomen conforming fairly close to a single type. Mayer proposed the subgenus *Chaetotelanocera* (probably a *lapsus* or typographical error for *Chaetotetanocera*) for *Tetanocera robusta* Loew, but I would consider such a group of no higher rank than any of the other species groups. The group with a single preapical posterior bristle

[2] Sabrosky (1951, Ent. Soc. Am., Ann., 44: 566–572) has shown what a confused state has prevailed in regard to the origin of the name *Tetanocera*, and that strict adherence to the Code would apply that name to the flies now known under the name *Dorycera* in the family Otitidae. The Sciomyzid genus would likely have to bear the name *Chaetomacera* Cresson 1920 or *Mycetomyza* Fallen 1810, which latter case would be unfortunate since the flies seem to have nothing to do with fungi. It seems to me that the most advantageous and simplest way out of this difficulty would be to designate *Tetanocera* a *nomen conservandum* based upon Tétanocère Duméril 1800, although a "vernacular" form, with *Musca elata* Fabr. as type, thus preserving the concept that has been current at least since Loew, 1847, and not disturbing the nomenclature of any other group.

on the middle femur and crossvein *tp* strongly sinuate (rubrics 5-17 of the following key) seems to be a natural one characteristic of the Nearctic region, although the Palaearctic *T. punctifrons* Rondani seems to fit into it. The Nearctic species *T. montana*, *T. soror*, *T. mallochi*, and *T. brevihirta* also seem to form a phylogenetic group. Further natural groups seem to be those similar to *T. rotundicornis* (*T. melanostigma*, *T. oxia*, and *T. spirifera*), the two forms with patterned wings (*T. valida* and *T. clara*), and the two Holarctic species *T. ferruginea* and *T. nigricosta*. I would hesitate to guess as to the relationships of these groups to each other and to the other species.

It is only recently that accurate separation of the species has been accomplished. Melander pointed the way in 1920 in first distinguishing species by the differences in the shape of the surstyli. Frey followed his lead in 1924, and Séguy and Verbeke continued the work, but even in the latest key to the Palaearctic forms (Mayer, 1953) there are a few species omitted, and figures of even parts of the male terminalia are still not available for nine species. Of the Nearctic species, figures of the surstyli of fourteen species, including the five Holarctic forms, were given by Melander, and I have published figures of the surstyli and a few additional details of five other species. I am trying herein to provide figures of the distinctive features of the male postabdomen of all of our forms, of which eight are described as new species. The female abdomen seems to provide nothing of moment.

The Male Postabdomen

I have shown in detail the complete postabdomen of two abundant species, *T. ferruginea* Fallén (Holarctic, Fig. 26) and *T. plebeia* Loew (Nearctic, Fig. 28). Recognition of the various parts of the other species may be had by comparison with these two. The figures are made with the dorsum downward, since examination in water or even of dry material is most natural in that position. Except as noted, the figures have been drawn from material macerated in NaOH solution and observed under water. Relaxation of dry material in a moist chamber, followed by manual extension of the postabdomen, is often sufficient for determination, but in critical cases, maceration is necessary to bring the structures into full view without distortion. It may be noted that frequently two views of the surstyli are practically necessary, and always give a much better conception of their

shape. The nomenclature is about the same as in my previous papers on the postabdomen.[3]

The protandrium (*pra*) is nearly symmetrical, the three somites of which it is composed being well fused and but little separated on the dextral side. The new species *T. stricklandi* (Fig. 30) shows the most nearly complete fusion of the somites 6, 7, and 8; the least complete fusion is found in several forms, such as *T. mallochi* (Fig. 17) and *T. plebeia* (Fig. 28). Commonly, all four spiracles of somites 6 and 7 are discernible. The shape of the protandrial sternite (synsternite) is frequently characteristic of the species. The surstyli (*ss*) are approximated to each other on the posterior margin of the epandrium and are the most easily observed and characteristic parts of the postabdomen. No anterior surstyli, such as occur in many Sciomyzinae, are discernible, unless a setose anterior part of the surstyli of several species may represent the remnant of such a part (cf. Figs. 1, 2, 26, 28).

The epandrium (*epa*) has its hind margins broadly fused on the mid-line between the surstyli and the anal structures, which occupy a position near the anterior margin of the sclerite. The line of fusion is sometimes entirely obliterated, sometimes indicated by a groove, and only in *T. stricklandi* shown by a strip of membrane. The shape of the ventral margin of the epandrium is specific.

The hypandrium (*hy*) and the structures connected with it have been called the inner copulatory apparatus (cf. Figs. 26*F* and 28*D*). The hypandrium is roughly U-shaped, open to the rear, where it is joined to a plate or pair of plates that seem to be sternite 10 (*10 S*). It is also attached to the anterior corners of the epandrium (at point *pa*) in such a way as to permit it to swing through a considerable arc. The hypandrium bears a pair of characteristically conformed, usually setose parts that I have called postgonites (*pg*). The processes anterior to the postgonites on each side are also highly characteristic of the species. The aedeagus (*ae*) is the only part of the postabdomen besides the protandrial sternite which is definitely asymmetrical; it is quite complex in a manner characteristic of the species, but I have not attempted to use it in separation of species. No spinus titillatorius seems to be developed in any species. The

[3] Steyskal, G. C., 1954. The American species of the genus Dictya Meigen (Diptera, Sciomyzidae), Ent. Soc. Am., Ann., 47: 511–539; 1957. The postabdomen of male acalyptrate Diptera, Ent. Soc. Am., Ann., 50: 66–73.

epandrium in one species, *T. robusta*, is asymmetrical (Figs. 1 and 3), with a protuberance on one side.

The closed abdomen of the male, made from fresh material in several instances, has been shown (Figs. 3, 4, 31 through 40) to assist in determining some of the species in the field or laboratory without manipulation.

Remarks on Characters Used in the Key

Although such characters as color, chaetotaxy, structure of the antennae, and venation are very useful, they are subject to considerable variation. Consequently, in almost all species certain individuals will be found whose determination must be made by examination of the postabdomen. A certain number of females also will be indeterminable.

The dark brown or black orbitoantennal spot is especially variable; sometimes in species not known to have such a spot a stain will develop in drying that can easily be mistaken for the true spot, and in species typically having the spot a goodly number of individuals will be found without it.

Some experience is necessary to use the character of the amount, length, and color of the aristal hairs with assurance, but with experience the character will become quite useful.

The stump-veins found in some species on the fourth vein are also variable. An indication of the extent of variation has been given under each species which has the stump-veins.

The hairs on the lower parafacials, when viewed at 90° to the face, are also useful. There are always some hairs near a line connecting the lower margins of the eyes; the distance in which hairs occur from that point toward a line even with the lower edge of the antennal sockets is relatively constant for each species.

The amount of brown coloring along the costal margin and to some extent in the apical cells of the wing, while seldom very great, is yet quite constant within each species.

KEY TO THE AMERICAN SPECIES OF *TETANOCERA*

1 (4). Posterior surface of middle femur with more than one bristle toward tip, usually about three; crossvein *tp* straight or but slightly arcuate or sinuate; wing without streaks or spots in cells and without stump-veins; prosternum bare or with a few setae; scutellum convex on dorsum; dark orbitoantennal spot lacking; dorsal profile of epandrium coarctate with that of protandrium (Figs. 3 and 4).

2 (3). Prosternum with a few setae; posterior femur with dorsal bristles on anterior side only; *male:* epandrium asymmetrical, with papilla on dextral side (Figs. 1, 3) ..... 1. *T. robusta* Loew

3 (2). Prosternum bare; posterior femur with posterodorsal preapical bristle; *male:* epandrium symmetrical, without papilla (Figs. 2, 4) ..... 2. *T. annae* Steyskal

4 (1). Posterior surface of middle femur without bristles or with but a single bristle near tip; *tp* straight to strongly sinuate; wings sometimes with dark markings in cells and often with stump-veins on fourth vein; posternum bare.

5(18). Posterior surface of middle femur with a single bristle near tip; *tp* strongly S-curved; scutellum somewhat flattened dorsally, with slight anterior ridge; *male:* epandrium in profile meeting protandrium at an angle (cf. Figs. 31, 32, at point marked by arrow).

6 (9). Parafacials with hairs well above mid-way between lower margin of eyes and border of antennal sockets; blackish orbitoantennal spot present; aristal hairs dense and black; abdomen with middorsal brown stripe; wings with distinct costal browning.

7 (8). Fourth vein normally with stump-veins.

a. Male terminalia as in Fig. 5 ..... 3. *T. vicina* Macquart

b. Surstylus as in Fig. 6 ..... 4. *T. iowensis* Steyskal

8 (7). Fourth vein nearly always lacking stump-veins; *male:* terminalia as in Figs. 7, 8 ..... 5. *T. nanciae* Brimley

9 (6). Parafacials with hairs extending less than halfway from lower margin of eyes to antennal sockets.

10 (11). Fore tarsi and apical 1/7 of tibiae black; aristal hairs sparse; abdomen with middorsal brown stripe; *male:* terminalia very small, with simple, curved surstyli (Mexico; Fig. 9) ..... 6. *T. spreta* Van der Wulp

11 (10). Fore tarsi and tibiae wholly tawny; abdomen dorsally unicolorous; *male:* terminalia larger.

12 (13). Aristal hairs especially dense and black; third antennal segment usually blackish at insertion of arista; orbitoantennal spot usually large and black; *male:* surstyli abruptly angulate apically (Fig. 13) ..... 10. *T. obtusifibula* Melander

13 (12). Aristal plumosity somewhat less dense; surstyli not abruptly angulate apically.

14 (15). Aristal plumosity dense and black; blackish orbitoantennal spot present; wings with strong costal browning; *male:* surstyli with straight basal margin; hypandrium with long posterior blade and rather long tooth just anterior to it (Fig. 10) ..... 7. *T. loewi*, sp. nov.

15 (14). Aristal plumosity rather sparse; orbitoantennal spot usually faint or lacking; wings without definite costal browning.

16 (17). *Male:* posterior process of hypandrium gently curved foreward; surstyli invaded by membrane at basal margin (Fig. 11) ..... 8. *T. mesopora*, sp. nov.

17 (16). *Male:* posterior process of hypandrium strongly curved forward; surstyli straight on basal edge (Fig. 12) ..... 9. *T. hespera*, sp. nov.

18 (5). Posterior surface of middle femur with small hairs only; *tp* straight, arcuate, or S-curved.

19 (22). Hind femur with posterodorsal bristle, opposite or nearly opposite to apical

anterodorsal bristle; aristal plumosity long but sparse. (N.B.: *T. plebeia* will sometimes fit this description; cf. rubric 35, Fig. 28).

20 (21). *Tp* S-curved; fourth vein without stump-veins; second antennal segment long; arista with long second segment; large species, wing 7.2–9.0 mm. long; *male:* postabdomen as in Fig. 16 ..... 13. *T. montana* Day

21 (20). *Tp* simply arcuate or straight; fourth vein nearly always with stump-veins; smaller species, wing 5.0–6.6 mm. long; *male:* postabdomen as in Fig. 20 ..... 17. *T. rotundicornis* Loew

22 (19). Hind femur without posterodorsal bristle; aristal plumosity various (cf. note at 19).

23 (26). Wings with brown spots or streaks on membrane besides costal browning or browning on fourth vein or crossveins; interfrontal stripe broad, polished, convex.

24 (25). No spots along fifth vein ..... 12. *T. clara* Loew

25 (24) Both sides of fifth vein with spots ..... 11. *T. valida* Loew

26 (23). Wings without spots in membrane, except sometimes streak in first posterior cell and cloud in second posterior cell.

27 (28). Interfrontal stripe not sharply demarcated but consisting of a broad, triangular, dully shining area anterior to ocelli; costal margin of wing not browned, but crossveins and more or less the ends of longitudinal veins margined with brown; stump-veins normally lacking ..... 20. *T. unicolor* Loew

28 (27). Interfrontal stripe more or less parallel-sided; if indistinct no dully shining triangular area is present.

29 (30). Anterior margin of front a little inflated, shining, connecting interfrontal and parafrontal shining stripes ..... 26. *T. silvatica* Meigen

30 (29). Anterior margin of frons matt.

31 (34). Interfrontal stripe narrow, ending well before anterior margin of frons or indistinct; wings unicolorous, without stump-veins, *tp* straight or slightly arcuate; *male*: dorsal protandrial profile rather squarish (Figs. 26, 27, 37, 38).

32 (33). Hairs of anterior front longer than diameter of an ocellus; arista with long, loose, and sparse hairs; *male:* surstyli with thin, erect, mediobasal laminae; fourth sternite lacking papillae (Fig. 26) ..... 23. *T. ferruginea* Fallén

33 (32). Hairs of anterior front indistinct, shorter than diameter of an ocellus; arista with short plumosity, second segment long; *male:* surstyli without laminae; protandrium with large anteroventral lobe; fourth sternite with a pair of setose papillae ..... 24. *T. bergi* Steyskal

34 (31). Interfrontal stripe well developed, extending to or nearly to anterior margin of frons; wings various.

N.B.: From this point on, sure determination is obtained only by examination of the male postabdomen.

35 (36). Interfrontal stripe broad, polished, attaining broadly anterior margin of frons; parafrontal stripes also broad and polished; orbitoantennal spot lacking in most specimens; aristal hairs long; second antennal segment approximately 0.7 length of the third segment; wings usually without stump-veins; second posterior cell usually with dark central cloud; *female:* medifacies shining, without pruinosity; *male:* surstyli with anterobasal patch of black setulae (Fig. 28). ..... 25. *T. plebeia* Loew

36 (35). Interfrontal and parafrontal stripes, although well developed, not especially shining nor broad; *female:* medifacies pruinose.

37 (38). Aristal hairs rather dense and black, longish; second antennal segment approximately 0.6 length of third segment, which is definitely concave on dorsal profile; parafacials with hairs at least halfway from lower margin of eyes to antennal sockets; orbitoantennal spot present; wings without stumps on fourth vein; *male:* protandrial sternite trilobate (Fig. 19).....16. *T. soror* Melander

38 (37). Aristal hairs sparser or shorter or paler; if rather dense and black, second antennal segment is less than half the length of the third segment, which is seldom concave in dorsal profile.

39 (40). Second segment of arista more than three times as long as wide; aristal hairs rather long but quite sparse; orbitoantennal spot lacking; wings without stump-veins; *male:* epandrium with strip of membrane mesally between surstyli and anus (Fig. 30).....27. *T. stricklandi*, sp. nov.

40 (39). Second segment of arista less than three times as long as wide; *male:* epandrium completely closed between surstyli and anus.

41 (44). Blackish orbitoantennal spot present; aristal hairs rather short (Figs. 17B, 24A); wings with costal browning, without stump-veins; thoracic dorsum without strong brown stripes.

42 (43). Wings with costal browning strong, including stigmal area; *tp* straight; *male:* postabdomen as in Fig. 24.....21. *T. spirifera* Melander

43 (42). Wings with weak costal browning, not including stigma; *tp* sinuate; *male:* postabdomen as in Fig. 17.....14. *T. mallochi* sp. nov.

44 (41). Orbitoantennal spot lacking. (*T. rotundicornis* will sometimes fit this description, cf. rubric 21).

45 (46). Aristal plumosity very short; wings without costal browning or stump-veins; *male:* postabdomen as in Fig. 18.....15. *T. brevihirta*, sp. nov.

46 (45). Aristal plumosity moderately long; wings with costal browning and usually with at least one stump-vein on the fourth vein.

47 (48). Second antennal segment 1.5 times as high as long, 0.42 length of third segment; wings with costal browning only distad of *ta*, usually with one stump-vein on posterior side of apical section of fourth vein, sometimes also on penultimate section; *male:* surstyli large, as in Fig. 25.....22. *T. nigricosta* Rondani

48 (47). Second antennal segment approximately as long as high, at least half as long as third segment; usually with at least one stump-vein on penultimate section of fourth vein, sometimes also on ultimate section; costal browning extending proximad to tip of auxiliary vein.

49 (50). Stigma light brown; dorsum of thorax with very faint stripes; *male:* surstyli acutely pointed, with mediobasal carina (Fig. 22).....19. *T. oxia*, sp. nov.

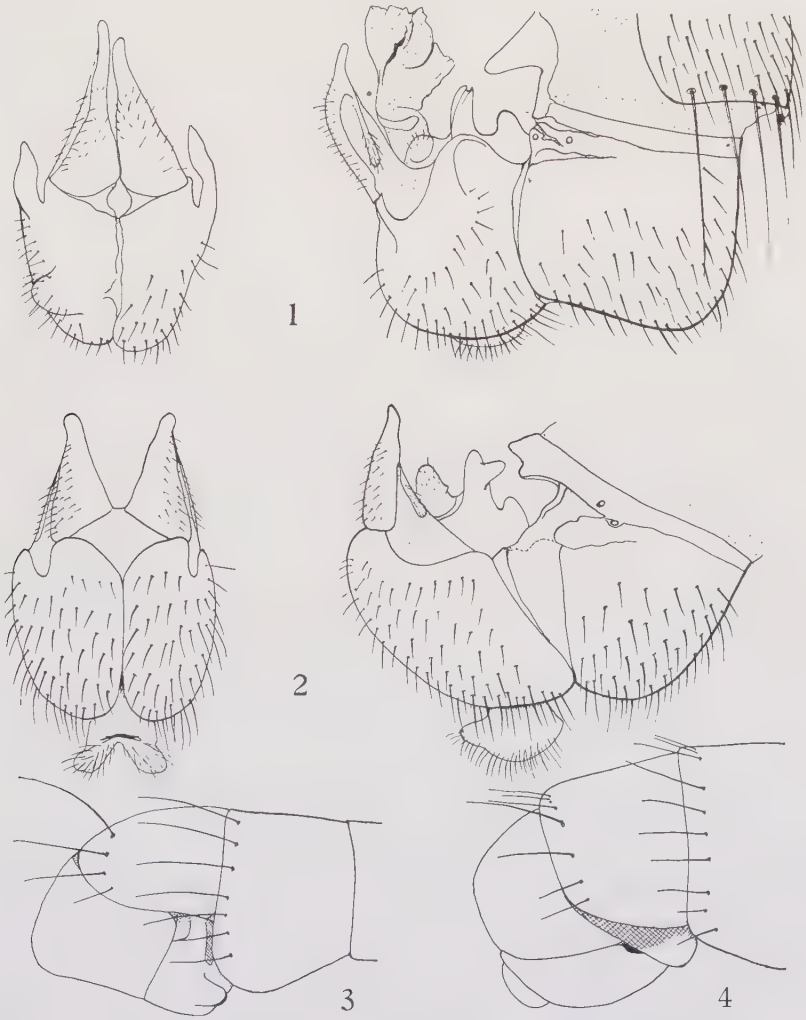
50 (49). Stigma dark brown; dorsum of thorax with distinct brown stripes; *male:* surstyli usually rounded at tip, without basal carina (Fig. 21).

18. *T. melanostigma*, sp. nov.

1. *Tetanocera robusta* Loew

(Figs. 1, 3)

1847, Stettiner Ent. Ztg., 8: 197; Engel, 1924, Zts. Wiss. Zool., 122: 516; Frey, 1924, Notulae Ent., 4: 51; Séguy, 1934, Faune de France, 28: 278; Strickland, 1946,



Abdomen of *Tetanocera* Species, Male

FIG. 1. *Tetanocera robusta* Lw., Custer, S. D., extended postabdomen.

FIG. 2. *T. annae* Stey., Grosse Ile, Mich., extended postabdomen.

FIGS. 3–4. Apical half of closed abdomen with only major bristles shown: 3. *T. robusta* Lw., Custer, S. D., dried specimen; 4. *T. annae* Stey., Alpena, Mich., fresh specimen.

Canadian Jour. Res., 24 (D): 168; Verbeke, 1948, Mus. Roy. Hist. Nat. Belg., Bull., 24: 21; Mayer, 1953, Naturhist. Mus. Wien., Ann., 59: 216 (as type of subgenus *Chaetotelanocera*); Steyskal, 1954, Ent. Soc. Washington, Proc., 56: 69.

Tetanocera papillifera Melander, 1920, Ent. Soc. Am., Ann., 13: 329 (syn. by Frey, 1924); Curran, 1928, Ent. Soc. Ontario, Ann. Rept., 58: 100.

This Holarctic species is one of the most easily recognized in both sexes by the setose prosternum and in the male by the protuberance on the right-hand side of the epandrium. It has been recorded in the literature from Alberta, Manitoba (Baldur; Victoria Beach; Winnipegosis), Washington (Pullman; Tacoma), Montana (Missoula), and Wyoming (Yellowstone Lake). I have seen material from Alaska (Anchorage; Kotzebue; Lower Yukon River; Matanuska Valley; Naknek Lake; Nome; Savonoski), British Columbia (Agassiz; Mission City; Vernon), Alberta (Calgary; Clymont; Gull Lake; Medicine Hat; Wabamun), Saskatchewan (Lisieux), Manitoba (Fort Churchill), Ontario (Lake Abitibi), Quebec (Cont. Paradis), Washington (Seattle; Yakima), Oregon (Portland), Utah (Hooper; Iron Co.; Logan; Ogden; Plain City); Montana (Summit Station), Wyoming (Lander; Yellowstone Park), Colorado (Pingree Park), New Mexico (Las Vegas), Wisconsin (Washburn Co.), South Dakota (Custer; Fort Pierre), Michigan (Isle Royale; Schoolcraft Co.).

2. *Tetanocera annae* Steyskal

(Figs. 2, 4)

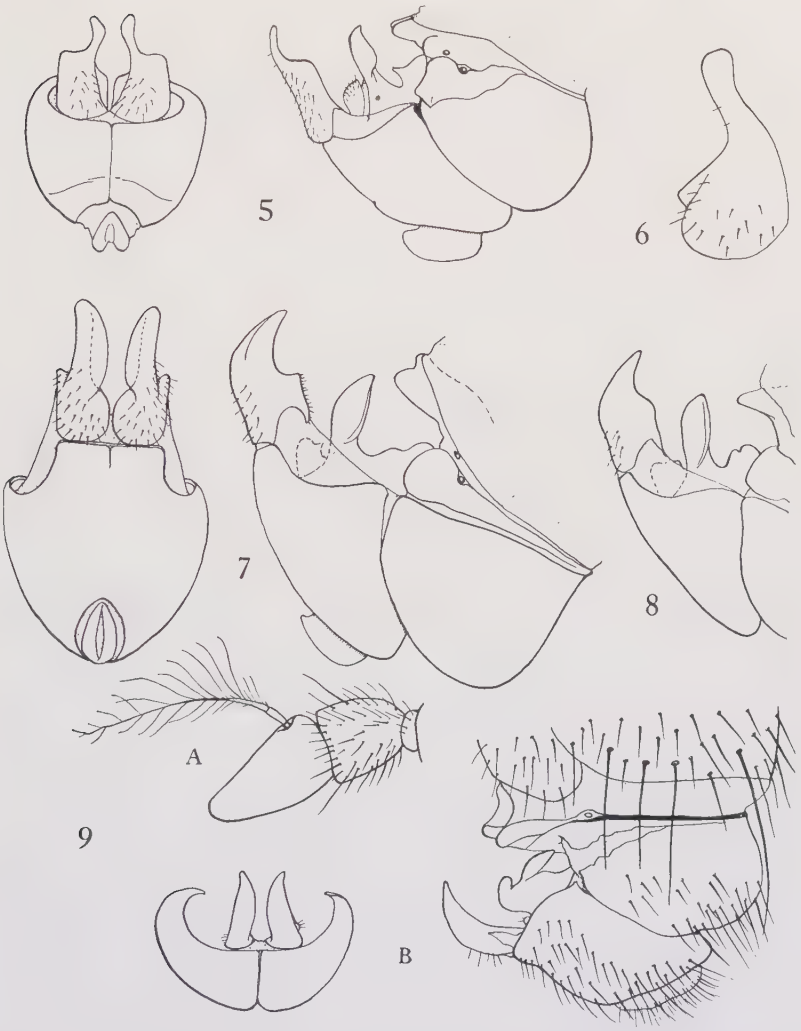
1938, Mus. Zool. Univ. Mich., Occas. Pap., 386: 5.

This easily recognized species has proved to be fairly abundant in the northeastern part of North America, but there is also a record from the northwest. I have seen material from the following localities: British Columbia (Agassiz), Ontario (Lobo; Ottawa), Wisconsin (Dane Co.; Madison; Shell Lake; Washburn Co.), Michigan (throughout, including Isle Royale), New York (Albion; Mt. McIntyre summit; North Fairhaven; Penn Yan), New Hampshire (Mt. Washington, summit flats).

3. *Tetanocera vicina* Macquart

(Figs. 5, 31)

1843, Dipt. Exot., 2(3): 180; Britton, 1920, Connecticut Geol. Nat. Hist. Surv. Bull., 31: 357; Melander, 1920, Ent. Soc. Am., Ann., 13: 327; Cole and Lovett, 1921, California Acad. Sci., Proc., (4) 11: 322; Malloch and McAtee, 1923, Ent. News,



Details of *Tetanocera* Species, Male

Fig. 5. *Tetanocera vicina* Macq., Grosse Ile, Mich., extended postabdomen, vestiture omitted from protandrium and epandrium.

Fig. 6. *T. iowensis* Stey., surstylus of holotype.

Figs. 7–8. *T. nanciae* Brim., extended postabdomen, vestiture omitted from protandrium and epandrium: 7. Specimen from Grand Traverse Co., Mich.; 8. Specimen from Keweenaw Co., Mich. (western form).

Fig. 9. *T. spreta* V. d. Wulp, Toluca, Mex.: *A*, antenna; *B*, extended postabdomen.

34: 233; Johnson, 1925, Boston Soc. Nat. Hist., Occas. Pap., 7: 252; 1925a, Boston Soc. Nat. Hist., Proc., 38: 95; 1927, Biol. Surv. Mt. Desert Reg., 1: 214; 1930, Nantucket Maria Mitchell Assn., Publ., 3 (2): 149; Petch and Maltais, 1932, Quebec Soc. Prot. Plants, 29th Rept., suppl.: 67; Brimley, 1938, Ins. No. Carolina: 379; Steyskal, 1938, Mus. Zool. Univ. Mich., Occas. Pap., 386: 4; Jaques, 1939, Iowa Acad. Sci., Proc., 45: 283; Knowlton, Harmston, and Stains, 1939, Utah Agric. Exper. Sta., Mimeogr. Ser. (Tech.), 200 (5): 13.

Chaetomacera vicina (Macquart) Cresson, 1920, Am. Ent. Soc., Trans., 46: 62.

The only species likely to be confused with *T. vicina* are *T. iowensis* and *T. nanciae*. The last-named lacks stump-veins, and *T. iowensis* differs in the shape of the surstylus and possibly in other features of the terminalia. Of thirty-three specimens of *T. vicina*, only one from Washburn County, Wisconsin, had no stump-veins at all, and another from Dane County, Wisconsin, has one stump-vein on the right wing only; all the others had at least one stump-vein on each wing, most typically about midway between *ta* and *tp* on the posterior side of the fourth vein. There may be as many as three stumps between the crossveins, two on the posterior side of the fourth vein and one on the anterior side; the average is close to 1.5. About 25 per cent of the wings have one (rarely two) stumps on the posterior side of the last section of the fourth vein also, and somewhat fewer also have a stump on either side of the vein proximad of the *ta* crossvein; when on the anterior side occasionally appearing as an additional *ta*.

There has been considerable confusion about the identity of *T. vicina*. The forms treated under that name by Cresson and Melander were certainly composite. As mentioned under *T. nanciae*, *T. plumosa* Loew is not a synonym of *T. vicina*.

I have seen specimens from a broad area in North America, as follows: British Columbia (Bear Lake; Mission City), Manitoba (Aweme), Ontario (Lake Abitibi; Orillia; Strathroy), Quebec (Cap Chat; Covey Hill; Gaspé Bay; Kingsmere; Knowlton; Quebec; Sweetsburg); New Brunswick (R. Gornis; Gornish), Washington (Mt. Constitution), Oregon (Corvallis), Idaho (Moscow), Utah (Miner's Peak, Iron Co.), Arizona (Greer), Colorado (Evergreen), South Dakota (Fort Pierre; Rapid City), Kansas (Saline Co.), Iowa (Jones Co.; Dickinson Co.), Wisconsin (Bayfield, Dane, Kenosha, Rusk, and Washburn Cos.), Illinois (Algonquin; Antioch; Carbondale; Channel Lake; Cypress; Peking; Ste. Anne; Urbana; Waterman), Michigan (throughout, including Isle Royale), Indiana (Lafayette),

Ohio (Cuyahoga Falls; Pickaway Co.), Tennessee (Knoxville), New York (Canton; Mt. McIntyre summit), New Jersey (Orange Mts.; Singac); Pennsylvania (Allegheny; Lehigh Gap; Milford), Maryland (Forest Glen), Virginia (Falls Church; Great Falls; Rosslyn), North Carolina (Raleigh), Connecticut (Canaan; Lyme Jct.), Massachusetts (Mt. Holyoke Gap).

4. *Tetanocera iowensis* Steyskal

(Fig. 6)

1938, Mus. Zool. Univ. Mich., Occas. Pap., 386: 4.

Besides the types from Jackson County, Iowa, and Ozark Mts., Van Buren, Missouri, the only other specimen I have seen is one in the United States National Museum from Boshertown, Missouri.

5. *Tetanocera nanciae* Brimley

(Figs. 7, 8, 32)

Tetanocera vicina nanciae Brimley, 1925, Ent. News, 36: 75.

T. nanciae (Brimley) Steyskal, 1938, Mus. Zool. Univ. Mich., Occas. Pap., 386: 4; Brimley, 1938, Ins. No. Carolina: 379; Jaques, 1939, Iowa Acad. Sci., Proc., 45: 283; Knowlton, Harmston, and Stains, 1939, Utah Agric. Exper. Sta., Mimeogr. Ser. (Tech.), 200 (5): 13; Strickland, 1946, Canadian Jour. Res., 24 (D): 168; Steyskal, 1954, Ent. Soc. Washington, Proc., 56: 68.

This may be *T. plumosa* Loew, but the type, which I saw a few years ago, is a female and may possibly be one of the closely related forms. I have seen Brimley's type, from Bryson City, North Carolina, and material from the following localities also—western material is somewhat different from the eastern and may deserve subspecific rank (cf. Fig. 8):

Alaska (Anchorage; Eagle River; Kadiak; Kukak Bay; Matanuska Valley; Nenana; Valdez), British Columbia (Agassiz; Atlin; Bowser; Chilliwack; Duncan; Hazelton; Kaslo; Mission City; Vernon), Alberta (Banff; Medicine Hat; Nordegg; Wabamun), Saskatchewan (Willows), Manitoba (Aweme; Mile 505, Hudsons Bay Railway), Ontario (Bobcaygeon; Bruce Peninsula; 10 miles east of Echo Bay; Elfrida; Golder Lake; Lake Abitibi; Penetang; Port Hope; Ottawa; Rondeau Park; Spenderville), Quebec (Mt. Albert; Beech Grove; Cascapedia; Kazabazua; Knowlton; New Richmond; Norway Bay), New Brunswick (R. Gornis), Nova Scotia (St. Peters), California (Big Meadows, San Bernardino Mts.; June Lake; Lake Tahoe; Mono

Co., 8500 ft.; Sta. Clara Co.; Tuolumne Co.), Nevada (Steamboat; Wells), Idaho (Moscow; Pollock; Potlatch), Utah (Coalville; Eden; Iron Springs; Logan; Plain City; Wellington), Arizona (Greer), Montana (Big Timber), Wyoming (Albany; Jackson; Parker Co.; Teton Co.; Yellowstone Park), Colorado (Eckert; Estes Park; Lake City; Pingree Park; Tennessee Pass), New Mexico ("N.M."), North Dakota (Lake Metigoshe, Turtle Mts.; Sioux Co.), South Dakota (Brookings; Custer; Lake Campbell; Plankinton), Minnesota (Jackson), Iowa (Dickinson Co.; Muscatine), Wisconsin (Dane, Door, and Washburn Cos.; Fish Creek; Green Bay), Illinois (Amboy; Mayview; Meredosia; Savanna; Urbana; Volo; Watseka; Waukegan), Michigan (abundant throughout, including Isle Royale), Ohio (Ross and Williams Cos.), New York (Ithaca; Long Id.), Pennsylvania (Glendale; Milford), North Carolina (Bryson City, holotype; Franklin; Raleigh), Massachusetts (Beverly), Vermont (Burke Mt. State Park), Maine (Carratunk).

6. *Tetanocera spreta* Van der Wulp

(Fig. 9)

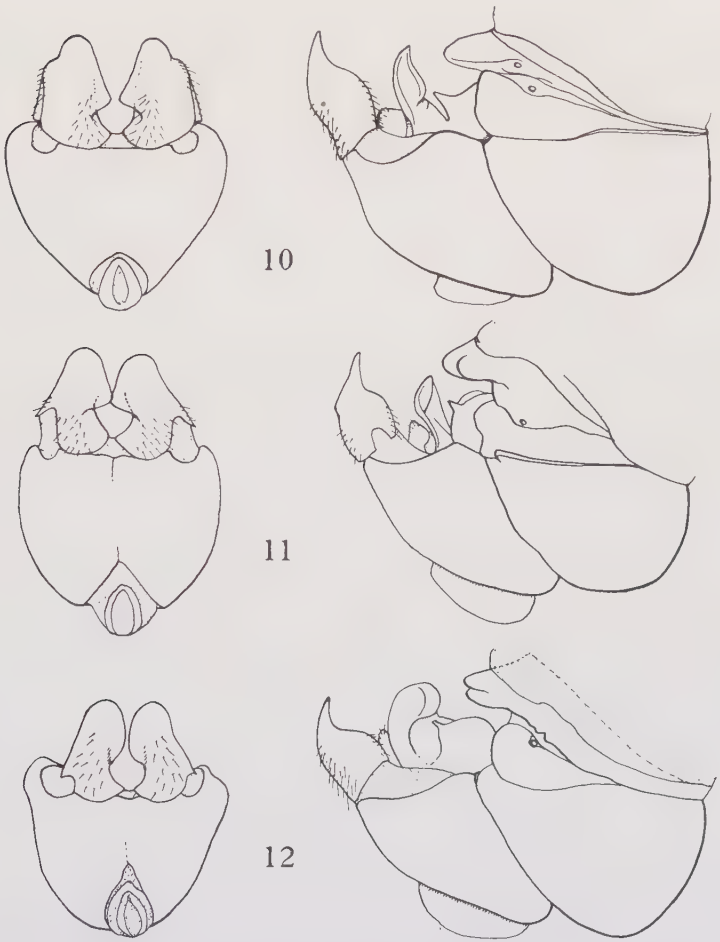
1897, Biol. Centr. Am., Dipt., 2: 359.

This easily distinguished form was found by Robert R. Dreisbach near Toluca, Mexico, August 17, 1954, 10,000 ft., and the figures were prepared from that specimen. Although I have not seen the type of *T. spreta* which was described from Jalisco and Mexico City, Mexico, Dreisbach's specimen agrees well with the description.

7. **Tetanocera loewi** Steyskal, sp. nov.

(Figs. 10, 32)

Male. Length of wing, 6.4 to 7.8 mm. In addition to the characters cited in the key, the bristles on the posteroventral surface of the fore femora are but little more than half as long as the greatest diameter of the femur and are much shorter in the basal third of the femur. The postabdomen (Fig. 10) is quite similar to those of *T. mesopora* and *T. hespera*, but the surstyli are somewhat differently shaped, the processes of the hypandrium are different, and the protandrial sternite differs. The surstyli are somewhat stouter than those of the other two species, the mesal flange extends farther basad, and the laterobasal margin is straight. The hypandrial processes



Extended Postabdomens of *Tetanocera* Species, Male

Fig. 10. *Tetanocera loewi*, sp. nov., paratopotype, Lapeer Co., Mich.
Fig. 11. *T. mesopora*, sp. nov., Washtenaw Co., Mich.
Fig. 12. *T. hespera*, sp. nov., holotype, Mendon, Utah.

(N.B.—Vestiture of protandrium and epandrium omitted from above and most of following figures.)

consist of a long process with a long lateral flange and a much shorter spur just anterior to it. The protandrial sternite has a straight free edge with rather abrupt squarish shoulders. The abdomen of this species when freshly captured is indistinguishable from that of *T. nanciae* (Fig. 32).

Female. Length of wing, 7.5 to 9.0 mm. The presence of the orbitoantennal spot, the strong costal browning of the wings, and the dense and black aristal plumosity will distinguish most female specimens.

Holotype (male) and allotype, Deerfield Township, Lapeer County, Michigan, July 10, 1954 (Geo. Steyskal). Paratypes of both sexes: Wisconsin (Madison; Rusk and Washburn Cos.), Michigan (Bay City; East Lansing; E. S. George Reserve, near Pinckney; Grosse Ile; Hamburg; Vineyard Lake, Jackson Co.; Branch, Cheboygan, Delta, Gratiot, Iosco, Isabella, Livingston, Manistee, Mecosta, Midland, Montcalm, and Wayne Cos.), Indiana (Bluffton), Ohio (Amherst), New York (Albion; Ithaca; McLean Bogs, Cortland Co.; Olcott; Spring Lake, Cayuga Co.), Ontario (Drummond; Marmora; Point Pelee; Rondeau Park, Kent Co.). The types and many paratypes are in my collection; other paratypes are in CNC, CU, MSU, RRD, UMMZ, USNM, and UW[4].

The distribution seems to be typically northeastern. *T. loewi* and the next two species have been confused under the name *T. triangularis*, which is, however, a synonym of *T. ferruginea*, q. v.

8. **Tetanocera mesopora** Steyskal, sp. nov.

(Fig. 11)

Male. Length of wing, 6.2 to 7.2 mm. In addition to the characters cited in the key, the bristles on the posteroventral are usually as long as the greatest diameter of the femora and are commonly developed almost to the base of the femora. The postabdomen (Fig. 11) differs in a few ways from those of *T. loewi* and *T. hespera*. The surstyli are somewhat smaller than those of *T. loewi*, the mesal

[4] Names of depositories have been abbreviated as follows: CNC, Canadian National Collection, Ottawa; CU, Cornell University, Ithaca, New York; MSU, Michigan State University, East Lansing; RRD, Robert R. Dreisbach collection, Midland, Mich.; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, United States National Museum, Washington, D.C.; UW, University of Wisconsin, Madison.

flange is shorter, and the laterobasal margin is more or less invaded by membrane. The hypandrial processes consist of a long, erect process with a rather short, lateral flange and a very small tooth anterior to it. The protandrial sternite has a straight, free edge with sloping shoulders. I have not seen fresh material, but dry material seems very much like *T. loewi* in the shape of the closed abdomen.

Female. Length of wing, 6.9 to 8.8 mm. The lacking or faint, orbitoantennal spot, absence of definite costal browning on the wings, loose and dark brown aristal plumosity, and long, fore femoral bristles will distinguish most females.

Holotype (male) and allotype, Walden, Colorado, 8,500 ft., Sept. 1–3, 1938 (C. L. Fluke). Paratypes of both sexes: Idaho (Moscow), Colorado (Walden; Grand Lake), North Dakota (Fort Yates), South Dakota (Plankinton; Waubay), Nebraska (Snake Falls, Cherry Co.), Wisconsin (Columbus; Madison; Dane and Washburn Cos.), Illinois (Chicago), Michigan (Douglas Lake; E. S. George Reserve, near Pinckney; Hart; Little Portage Lake, Washtenaw Co.; Nottawa; Clare, Lake, and Wexford Cos.), New York (Cedarville), Saskatchewan (Willows), Ontario (Iroquois; Ottawa), Quebec (Cascapedia). Type and paratypes in my collection; other paratypes in CNC, CU, MSU, RRD, UMMZ, USNM, UW.

The distribution is thus more western and northern than that of *T. loewi.* This is also a species that has gone under the name *T. triangularis.*

9. **Tetanocera hespera** Steyskal, sp. nov.

(Fig. 12)

Male. Length of wing, 6.5 to 7.3 mm. In addition to the characters cited in the key, the bristles on the posteroventral surface of the fore femora are but little developed, much less than half as long as greatest diameter of the femora. The postabdomen (Fig. 12) differs in a few ways from those of *T. loewi* and *T. mesopora.* The surstyli are somewhat smaller than those of *T. loewi* and the mesal flange shorter, but the laterobasal margin is straight also. The hypandrial processes are distinctive, the long process strongly curved forward with rounded tip, the small tooth anterior to it somewhat turned posterad. The protandrial sternite has a straight, free margin with knobby shoulders that extend a little laterad. No fresh material has been examined, but the dry material leads me to believe

that the closed abdomen must be very like those of *T. loewi* and *T. mesopora*.

Female. I have seen only one female that I could consider to be *T. hespera*, from Belcourt, Rollette County, North Dakota. The only character to distinguish it from *T. mesopora* seems to be the short bristles of the fore femora.

Holotype, male, Mendon, Utah, August 11, 1937 (G. F. Knowlton and W. P. Nye). Paratypes (male): Alaska (Anchorage; Lower Tonsina; Matanuska Valley; Palmer), Alberta (Banff; Wabamun), Washington (Olga), Utah (Cache Junction; Mendon), South Dakota (Custer). Type and paratypes in my collection; other paratypes in CNC, CU, USNM.

This is evidently a species of northwestern distribution. It also has gone under the name *T. triangularis*.

10. *Tetanocera obtusifibula* Melander

(Fig. 13)

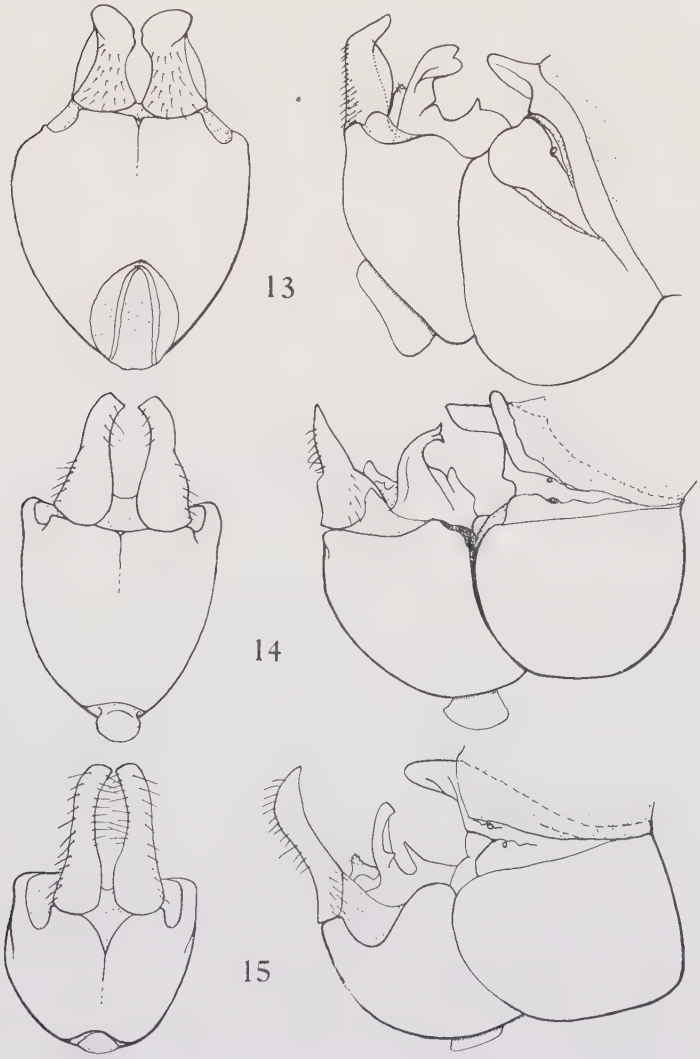
1920, Ent. Soc. Am., Ann., 13: 328.

Melander's type material was from Pullman and Mt. Constitution, Washington, Worley, Idaho, and Stanford, California. The surstylus from which his figure was prepared was apparently subjected to flattening. I have seen only a relatively small amount of material from the following localities. Washington (Rochester; Union Flat), Oregon (Cascadia; Corvallis; Kiger's Id.), California (Fort Seward; Paradise Cove, Marin Co.; Stanford), Idaho (Moscow), British Columbia (Royal Oak). There is a specimen from Berthierville, Quebec, in the Ouellet collection at the University of Montreal, determined by Guy Shewell.

11. *Tetanocera valida* Loew

(Fig. 14)

1862, Monogr. Dipt. No. Am., 1: 110; Aldrich, 1905, Smithsonian Misc. Coll., 46 (Cat. No. Am. Dipt.): 580; Van Duzee, 1911, Canadian Ent., 43: 243; Walker, 1913, Nat. Hist. Toronto Reg.: 395; Gibson, 1916, Ent. Soc. Ont., Ann. Rept., 46: 218; Britton, 1920, Connecticut Geol. Nat. Hist. Surv. Bull., 31: 201; Melander, 1920, Ent. Soc. Am., Ann., 13: 326; Johnson, 1925, Boston Soc. Nat. Hist., Proc., 38: 95; 1925a, Boston Soc. Nat. Hist., Occas. Pap., 7: 252; Leonard, 1928, Cornell Univ. Agric. Exper. Sta. Mem., 101: 847; Johnson, 1927, Biol. Surv. Mt. Desert Reg.; pt. 1: 214; 1930, Nantucket Maria Mitchell Assn., Publ., 3: 149; Curran, 1930, Am. Mus. Nat. Hist., Bull., 61: 82; Petch and Maltais, 1932, Quebec Soc.



Extended Postabdomens of *Tetanocera* Species, Male

Fig. 13. *Tetanocera obtusifibula* Mel., Cascadia, Ore.
Fig. 14. *T. valida* Lw., Iron Co., Mich.
Fig. 15. *T. clara* Lw., Mitchell Co., N. C.

Prot. Plants, 29th Rept., suppl.: 67; Knowlton, Harmston, and Stains, 1939, Utah Agric. Exper. Sta., Mimeogr. Ser., 200 (Tech.) (5): 13; Strickland, 1946, Canadian Jour. Res., 24 (D): 168.

Chaetomacera valida (Loew) Cresson, 1920, Am. Ent. Soc., Trans., 46: 57.

This very easily recognized species is known from the literature and from material I have seen from the following localities—it is considerably more abundant and widespread than its nearest congener, *T. clara*:

British Columbia (Agassiz; Likely), Alberta (Edmonton; Vermillion), Saskatchewan (Kenosee; Rockglen; St. Victor; Wood Mt.), Manitoba (Aweme; Carberry; Roblin; Teulon), Ontario (Blackburn; Eldorada, Hastings Co.; Kearney; Lake Abitibi; Lake Simcoe; Ottawa; Toronto; Westree), Quebec (Aylmer; Brome Co.; Cap Chat; Covey Hill; Foster; Hemmingford; Joliette; Knowlton; Lac Mondor, Ste. Flore; Lauzon; Longueuil; Megantic; Montreal; Quebec; Ottawa district; St. Hilaire; Ste. Therese Jct.), New Brunswick (R. Gornis), Nova Scotia (Kentville), Utah (Logan), Wyoming ("Wyoming"), Colorado ("Colorado"), New Mexico (Arroyo Pecos R.), Minnesota (Duluth), Wisconsin (Brule R.; Madison; Dane, Rusk, and Washburn Cos.), Illinois ("Illinois"), Michigan (throughout, including Isle Royale), New York (Erie Co.; Ithaca; Manlius; Dug Mt., Adirondacks; Tuxedo; West Nyack), Pennsylvania (Hazleton; La Plume), Connecticut (Danbury), Rhode Island (Buttonwoods), Massachusetts (Auburndale; Bashbish Falls; Brookline; Gloucester; Nantucket Id.), Vermont (St. Johnsbury); New Hampshire (Mt. Washington), Maine (Capens; Machias; Mt. Desert region).

12. *Tetanocera clara* Loew

(Fig. 15)

1862, Monogr. Dipt. No. Am., 1: 109; Aldrich, 1905, Smithsonian Misc. Coll., 46 (Cat. No. Am. Dipt.): 579; Smith, 1910, New Jersey St. Mus., Ann. Rept. for 1909: 797; Britton, 1920, Connecticut Geol. Nat. Hist. Surv. Bull., 31: 201; Melander, 1920, Ent. Soc. Am., Ann., 13: 326; Malloch and McAtee, 1923, Ent. News 34: 233; Johnson, 1925, Boston Soc. Nat. Hist., Occas. Pap., 7: 252; 1927, Biol. Surv. Mt. Desert Reg., pt. 1: 214; Leonard, 1928, Cornell Univ. Agric. Exper. Sta. Mem., 101: 847; Curran, 1930, Am. Mus. Nat. Hist., Bull., 61: 82; Petch and Maltais, 1932, Quebec Soc. Prot. Plants, 29th Rept., suppl.: 67; Brimley, 1938, Ins. No. Carolina: 379.

Chaetomacera clara (Loew) Cresson, 1920, Am. Ent. Soc., Trans., 46: 58.

This species is also very easily recognized. It is a little less abundant and more restricted in its range than *T. valida*. Records

and material I have seen indicate the following distribution: Quebec (Joliette; Montreal), Wisconsin (Columbus), Illinois (State Forest, Jonesboro), Michigan (Ingham, Kalamazoo, Kalkaska, Keweenaw, Marquette, Mecosta, Oceana, and Washtenaw Cos.), Ohio (Amherst), Tennessee (Clingman's Dome), Georgia (Atlanta; Blood Mt.), New York (Elmira; Johnstown; Lake Placid; Long Id.; Poughkeepsie; Saranac Inn; Speculator; Trenton Falls; Tuxedo; Upper Ausable Lake; Wells; West Nyack), New Jersey (Atco; Clementon; Delaware Water Gap; Dunnfield; Merchantsville; New Hope; Riverton), Pennsylvania (Castle Rock; Germantown; Glenside; Olney; Roxborough), Maryland (Plummer's Id.), District of Columbia, Virginia (Dead Run; Great Falls; Skyland), North Carolina (Murfreesboro; Penland, Mitchell Co.; Raleigh; Swannanoa), Connecticut, Massachusetts (Brookline), Vermont, New Hampshire (Bretton Woods; Mt. Washington), Maine (Mt. Desert Region).

13. *Tetanocera montana* Day

(Figs. 16, 33)

1881, Canadian Ent., 13: 87; Melander, 1920, Ent. Soc. Am., Ann., 13: 328; Steyskal' 1954, Ent. Soc. Washington, Proc., 56: 67.
Tetanocera montanae (Day) Strickland, 1946, Canadian Jour. Res., 24 (D): 168.

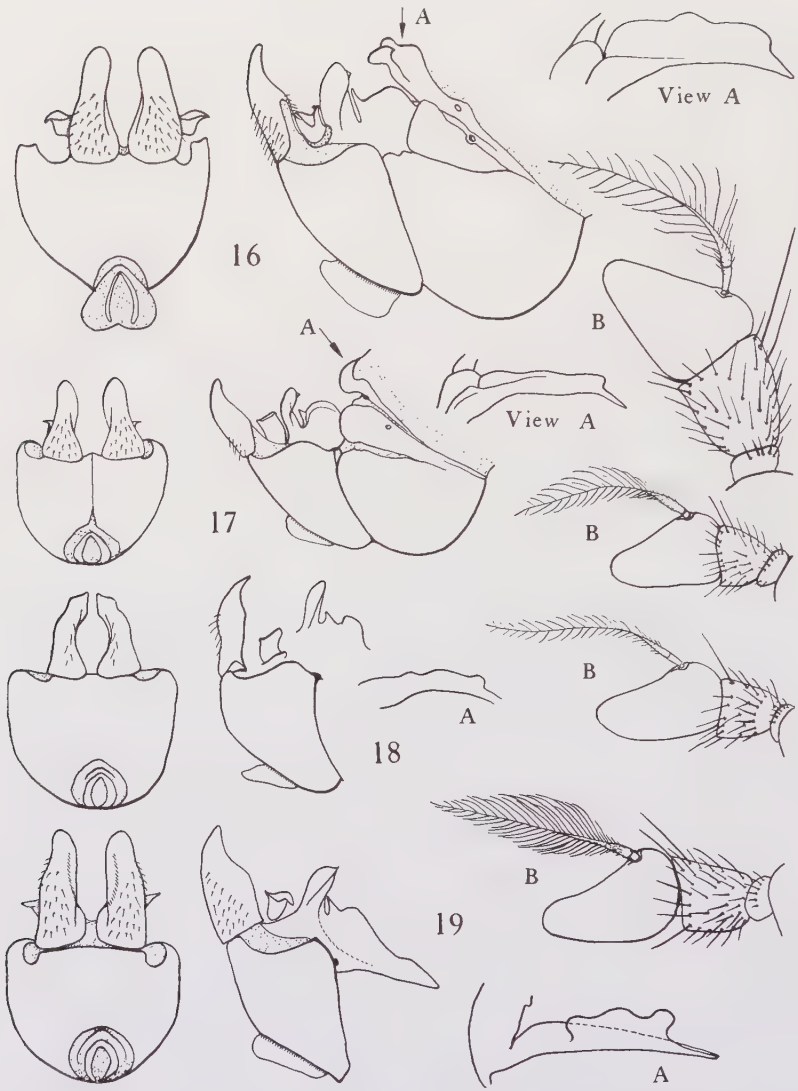
The characters cited in the key and those of the male postabdomen should make determination of this species fairly simple. But there has been considerable confusion in the determinations in various collections. I have seen material from the following localities:

Alaska (Eklutna; Matanuska Valley), Yukon Territory (Haines Jct.), British Columbia (Altin), Alberta (Wabamun), Manitoba (Churchill; mile 505, Hudsons Bay Railway), Ontario (Marmora; Ottawa), Wisconsin (Sturgeon Bay; Rusk and Washburn Cos.), Michigan (Alpena; East Lansing; Delta, Dickinson, Gladwin, Mackinac, and Washtenaw Cos.), New York (Albion).

14. **Tetanocera mallochi** Steyskal, sp. nov.

(Figs. 17, 36)

Male. Length of wing, 4.7 to 5.5 mm. All characters that I can find which will serve to distinguish this species from its relatives are mentioned in the key or shown in the figures. The wings have considerable browning of the costa apically, the crossveins are both strongly infuscated; in the first posterior cell is a brownish streak and



Extended Postabdomens and Antennae of *Tetanocera* Species, Male

Fig. 16. *Tetanocera montana* Day, Alpena, Mich.
Fig. 17. *T. mallochi*, sp. nov., holotype, Fort Churchill, Man.
Fig. 18. *T. brevihirta*, sp. nov., holotype, Fairbanks, Alaska.
Fig. 19. *T. soror* Mel., Mt. Constitution, Wash. *A*, ventral view of protandrial sternite; *B*, antenna.

in the second posterior cell, a cloud. The *tp* crossvein is somewhat sinuate, but not strongly, as in the *T. nanciae* group. The postabdomen is most characteristic: the surstyli have a mesal flange starting approximately at mid-length; the postgonites are truncate apically, with a sharp edge turned laterally when the aedeagus is fully extended; the hypandrium has the long process somewhat turned forward, with a lateral flange, and there is a well-marked ventral flange on the lobe anterior to the long process; and the protandrial sternite has the free margin nearly straight (Fig. 17, view A). The closed abdomen of a dry specimen is shown in Figure 36. There is a distinct step between the protandrium and epandrium, the former quite round in profile, and the whole abdomen roughly cylindrical and without very large bristles.

Female. Length of wing, 5.4 to 7.0 mm. Distinguished as in the key. Some have a few short or indistinct stump-veins.

Holotype (male) and allotype, Fort Churchill, Manitoba, July 21, 1952 (J. G. Chillcott). Paratypes of both sexes: Alaska (King Salmon, Naknek R.; Nebesna; Polychrome Pass; Richardson Highway, milepost 183), Northwest Territories (Aklavik; Muskox Lake, 64° 45′ N., 108° 10′ W.; Salmita Mines, 64° 05′ N., 111° 15′ W.), Alberta (Banff Nat. Park, Sunwapta Pass, 6700 ft.), Manitoba (Fort Churchill; mile 505, Hudsons Bay Railway), Quebec (Indian House Lake), Labrador (Hebron), New Hampshire (White Mts.). The types and several paratypes are in CNC; other paratypes are in my collection, CU, and USNM.

This species is dedicated to John R. Malloch in appreciation of the assistance he lent me in the early days of my study of the Sciomyzidae. It is possible that *T. brevisetosa* Frey may be either this form or the following one, but examination of authentic material from Europe will be necessary to decide.

15. **Tetanocera brevihirta** Steyskal, sp. nov.

(Fig. 18)

Male. Length of wing, 5.6 mm. The characters cited in the key and the figure should easily distinguish this species. The aristal plumosity is shorter than in any other species I have seen. The postabdominal features are also quite distinctive, the surstyli alone being unlike any other form.

Female. Length of wing, 6.7 mm. Distinguished as in the key.

Holotype (male), July 2, and allotype, July 4, 1921, Fairbanks, Alaska (J. M. Aldrich), in USNM.

The key will show the relationships of *T. brevihirta* to the other North American species. It is possible that this form or the preceding one is the same as *T. brevisetosa* Frey.

16. *Tetanocera soror* Melander

(Fig. 19)

1920, Ent. Soc. Am., Ann., 13: 328.

This rare form was described from Mica, Washington, with paratypes from Pullman and Mt. Constitution, Washington; Avon, Idaho; and Beaver Creek, Montana. I have seen only a few specimens from Mt. Constitution (from one of which the figure was drawn), Wells, Nevada, and Corvallis, Oregon. The species is quite evidently one of a group with *T. montana*, *T. mallochi*, and *T. brevihirta*, but the heavily long-plumose arista and the distinctly trilobata free edge of the protandrial sternite are unique in that group.

17. *Tetanocera rotundicornis* Loew

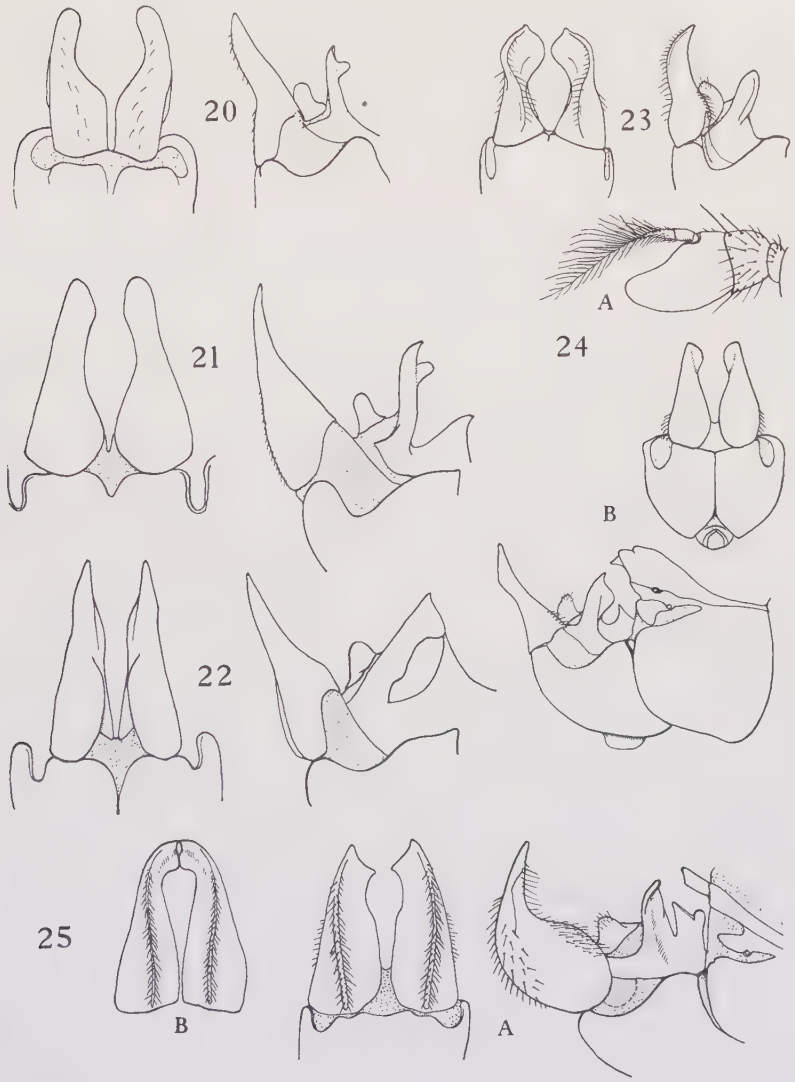
(Fig. 20)

1861, Berlin. Ent. Zts., 5: 344 (Cent. 1, no. 70); 1862, Monogr. Dipt. No. Am., 1: 23; Aldrich, 1905, Smithsonian Misc. Coll., 46 (Cat. No. Am. Dipt.): 580; Walker, 1913, Nat. Hist. Toronto Reg.: 395; Britton, 1920, Connecticut Geol. Nat. Hist. Surv. Bull., 31: 61; Melander, 1920, Ent. Soc. Am., Ann., 13: 328; Johnson, 1925, Boston Soc. Nat. Hist., Occas. Pap., 7: 252; 1927, Biol. Surv. Mt. Desert Reg., pt. 1: 215; Leonard, 1928, Cornell Univ. Agric. Exper. Sta. Mem., 101: 847; Curran, 1930, Am. Mus. Nat. Hist., Bull., 61: 82; Petch and Maltais, 1932, Quebec Soc. Prot. Plants, 29th Rept., suppl.: 67; Brown, 1934, Canadian Ent., 66: 252; Steyskal, 1954, Ent. Soc. Washington, Proc., 56: 69.

Chaetomacera elata var. *rotundicornis* (Loew) Cresson, 1920, Am. Ent. Soc., Trans., 46: 61.

The type series is likely mixed, only a female showing the characteristic stump-veins on the fourth vein; it will cause the least disturbance to the nomenclature to consider that specimen the holotype. Confusion has existed between this form and those described below as *T. melanostigma* and *T. oxia*. Loew's material was collected by Kennicott at English River, western Ontario. I have seen specimens from the following localities:

Alaska (Lower Yukon River; Matanuska Valley; Naknek River; Palmer Highway, mile 40); Quebec (Cascapedia; New Richmond;



Extended Postabdomens and Antenna of *Tetanocera* Species, Male

Fig. 20. *Tetanocera rotundicornis* Lw., Matanuska Valley, Alaska.

Fig. 21. *T. melanostigma*, sp. nov., Grand Traverse Co., Mich.

Fig. 22. *T. oxia*, sp. nov., holotype, Sanilac Co., Mich.

Fig. 23. *T. unicolor* Lw., Quebec, Que.

Fig. 24. *T. spirifera* Mel., Atlin, B. C.: *A*, antenna; *B*, postabdomen.

Fig. 25. *T. nigricosta* Rond., Naknek R., Alaska; *A*, specimen with short-tipped surstyli; *B*, extreme variant with long-tipped surstyli.

Quebec), Ontario (Ancaster), Wisconsin (Dane Co.), Illinois (Lake Villa, swamp), Michigan (Isle Royale; New Baltimore; Charlevoix, Midland, Osceola, and Roscommon Cos.), New York (Albion).

18. **Tetanocera melanostigma** Steyskal, sp. nov.

(Figs. 21, 34)

Male. Length of wing, 5.6 to 6.5 mm. The characters cited in the key will serve to separate this form, and the figure of the postabdomen will present additional important characters, one of the most conspicuous of which is the angular emargination of the ventral margin of the epandrium. The closed abdomen of a fresh male specimen is shown in Figure 34. The blackish stigma will help separate this form from *T. oxia* and *T. rotundicornis.* The fourth vein of the wing usually has a few stump-veins. Twenty-three specimens, with a total of 45 wings (1 missing), showed an average of 1.6 stumps per wing; 4 wings had no stumps at all; the largest number of stumps was 5, 1 proximad of the crossveins, 3 between the crossveins, and 1 distad of *tp.*

Female. Length of wing, 6.0 to 7.4 mm. Distinguished as in the key.

Holotype (male), May 29, and allotype, May 31, 1957, Dryden, New York (Geo. Steyskal). Paratypes of both sexes: Ontario (Elfrida; Marmora; Midland; Rondeau Park, Kent Co.), Quebec (Cap Chat; Mt. Albert), Michigan (E. S. George Reserve, near Pinckney; Gull Lake Biol. Sta., Kalamazoo Co.; Grand Traverse, Lapeer, and Sanilac Cos.), New York (Axton; Babylon; Cold Spring Harbor; Dryden; Ellis; Ithaca; Juanita Id., Lake George; Ontario Beach, N. Fairhaven; Patterson; Rock City; Slide Mt., Ulster Co.), New Hampshire (N. Haverhill). The types and several paratypes are in my collection; other paratypes are in CNC, CU, MSU, and USNM.

19. **Tetanocera oxia** Steyskal, sp. nov.

(Fig. 22)

Male. Length of wing, 4.7 to 5.8 mm. The characters cited in the key and the acutely pointed surstyli with a low mediobasal carina will distinguish this species from *T. melanostigma* and *T. rotundicornis.* The ventral margin of the epandrium is arcuately emarginate. The

stigma is only lightly browned. Of the 26 available wings, only 1 had 2 stump-veins, 1 on either side of the fourth vein between the crossveins; 3 pairs and 1 odd wing had no stumps at all; all the rest had 1 stump or at least an indication of a stump on the posterior side of the fourth vein between the crossveins.

Female. Unknown.

Holotype (male), Sanilac Co., Michigan, May 30, 1952 (Geo. Steyskal). Paratypes: Saskatchewan (Saskatoon), Alberta (Fawcett), Michigan (Detroit; Cheboygan, Midland, and Tuscola Cos.). The type and several paratypes are in my collection; other paratypes are in CNC, RRD, and UMMZ.

20. *Tetanocera unicolor* Loew

(Figs. 23, 39)

1847, Stettiner Ent. Ztg., 8: 199; Hendel, 1900, Zool.-bot. Ges. Wien, Verhandl., 50: 337; 1903, Zts. Hymen. Dipt., 1: 37; Melander, 1920, Ent. Soc. Am., Ann., 13: 328; Frey, 1924, Notulae Ent., 4: 53; Johnson, 1925, Boston Soc. Nat. Hist., Occas. Pap., 7: 252; 1927, Biol. Surv. Mt. Desert Reg., pt. 1: 215; Petch and Maltais, 1932, Quebec Soc. Prot. Plants, 29th Rept., suppl.: 67; Séguy, 1934, Faune de France, 28: 280; Jaques, 1939, Iowa Acad. Sci., Proc., 45: 283; Sack, 1939, in Lindner, Die Fliegen d. pal. Reg., 5 (fasc. 37): 54; Ouellet, 1941, Le Nat. Canadien, 68: 135; Verbeke, 1948, Mus. Roy. Hist. Nat. Belg., Bull., 24: 21; Mayer, 1953, Naturhist. Mus. Wien, Ann., 59: 208; Steyskal, 1954, Ent. Soc. Washington, Proc., 56: 70.

Chaetomacera unicolor (Loew) Cresson, 1920, Am. Ent. Soc., Trans., 46: 59.

This rather easily recognized form, described from Europe, has been recorded from the following places in North America: Quebec (Val d'Espoir, vic. Percé, Gaspesia; Hull), by Ouellet and Petch and Maltais, respectively; Maine (Fort Kent; Machias; Mt. Desert), by Johnson. I have seen specimens, including some serving as the basis for published records, from the following localities:

Alaska (Anchorage; Cold Bay; Eagle River; King Salmon; Matanuska Valley; Palmer Highway, mile 16; Popoff Id.; Tanana; Thane; Virgins Bay), British Columbia (Canim Lake), Alberta (Banff Nat. Park), Manitoba (Churchill; Victoria Beach; mile 505, Hudsons Bay Railway), Ontario (Ottawa), Quebec (Kazabazua; Mt. Albert; Quebec), New Brunswick (Barber D.), Arizona (Greer), Montana (West Yellowstone), Wyoming (Jackson, 6,000 ft.), North Dakota (Rollette and Sioux Cos.), Iowa (Dickinson Co.), Wisconsin (Madison; Price Co.), Michigan (Isle Royale; St. Ignace; Alcona,

Baraga, Delta, Iron, Keweenaw, Livingston, Roscommon, and Wexford Cos.), New York (White Church, Tompkins Co.), Maine (Ft. Kent).

21. *Tetanocera spirifera* Melander

(Figs. 24, 40)

1920, Ent. Soc. Am., Ann., 13: 330.

Melander described this interesting little form from Powell County and Gardiner, Montana. As will be seen from a comparison of the figures, it is related to the *T. rotundicornis*, *T. melanostigma*, and *T. oxia*. A sketch of a typical abdomen of a dry specimen is shown in Figure 40; the large protandrium with a noselike hump should be noted.

I have seen material from the following localities: Northwest Territories (Salmita Mines, 64° 05′ N., 111° 15′ W.), British Columbia (Atlin), Alberta (Banff Nat. Park), Saskatchewan (Rockglen; Scout Lake), Manitoba (Ft. Churchill; mile 505, Hudsons Bay Railway), North Dakota (Minot), South Dakota (Waubay; Erwin).

22. *Tetanocera nigricosta* Rondani

(Fig. 25)

1868, Soc. Ital. Sci. Nat. Milano, Atti, 11: 223; Hendel, 1900, Zool.-bot. Ges. Wien, Verhandl., 50: 342 (as extreme form of *T. elata*); Séguy, 1934, Faune de France, 28: 280; Verbeke, 1948, Mus. Roy. Hist. Nat. Belg., Bull., 24: 22; Mayer, 1953, Naturhist. Mus. Wien, Ann., 59: 208.

Tetanocera phyllophora Melander, 1920, Ent. Soc. Am., Ann., 13: 330; Strickland, 1946, Canadian Jour. Res., 24 (D): 168; Steyskal, 1954, Ent. Soc. Washington, Proc., 56: 68. *New Synonym.*

Séguy was the first adequately to distinguish this form from its relatives. I have compared a specimen from Belgium received through the kindness of Jean Verbeke and find the post-abdomen the same as those of specimens determined as *T. phyllophora*. Our material usually has a stump-vein on the posterior side of the last section of the fourth vein and sometimes an additional one between the crossveins, but no such stumps have been noted for European material. Strangely enough, Melander did not mention stumps in his unique type specimen either, and specimens lacking stumps are not uncommon in North America. Séguy's character of the lack of propleural setae does not hold for our material and was not used by Verbeke and Mayer.

Melander's type was from Mt. Constitution, Washington. I have seen North American material from the following places: Alaska (Anchorage; Fairbanks; King Salmon, Naknek River; Lower Yukon River, Holy Cross; Matanuska Valley), British Columbia (Kaslo), Alberta (Edmonton; Fawcett; Gull Lake; Wabamun; Wetawiskin), Ontario (Lake Abitibi), Nova Scotia (Truro), Colorado (Pike's Peak), New Mexico (Cimarron Canyon, Colfax Co.), Michigan (Copper Harbor; Isle Royale), Vermont (Mt. Mansfield summit), New Hampshire (White Mts.).

23. *Tetanocera ferruginea* Fallén

(Figs. 26, 37)

1820, Sciomyzides Sveciae: 9; Loew, 1847, Stettiner Ent. Ztg., 8: 197; Hendel, 1900, Zool.-bot. Ges. Wien, Verhandl., 50: 339; 1903, Zts. Hymen. Dipt., 1: 37; Melander, 1920, Ent. Soc. Am., Ann., 13: 327; Frey, 1924, Notulae Ent., 4: 51; Séguy, 1934, Faune de France, 28: 279; Sack, 1939, in Lindner, Die Fliegen d. pal. Reg., 5 (fasc. 37): 51; Verbeke, 1948, Mus. Roy. Hist. Nat. Belg., Bull., 24: 22; Mayer, 1953, Naturhist. Mus. Wien, Ann., 59: 208; Steyskal, 1954, Ent. Soc. Washington, Proc., 56: 67.

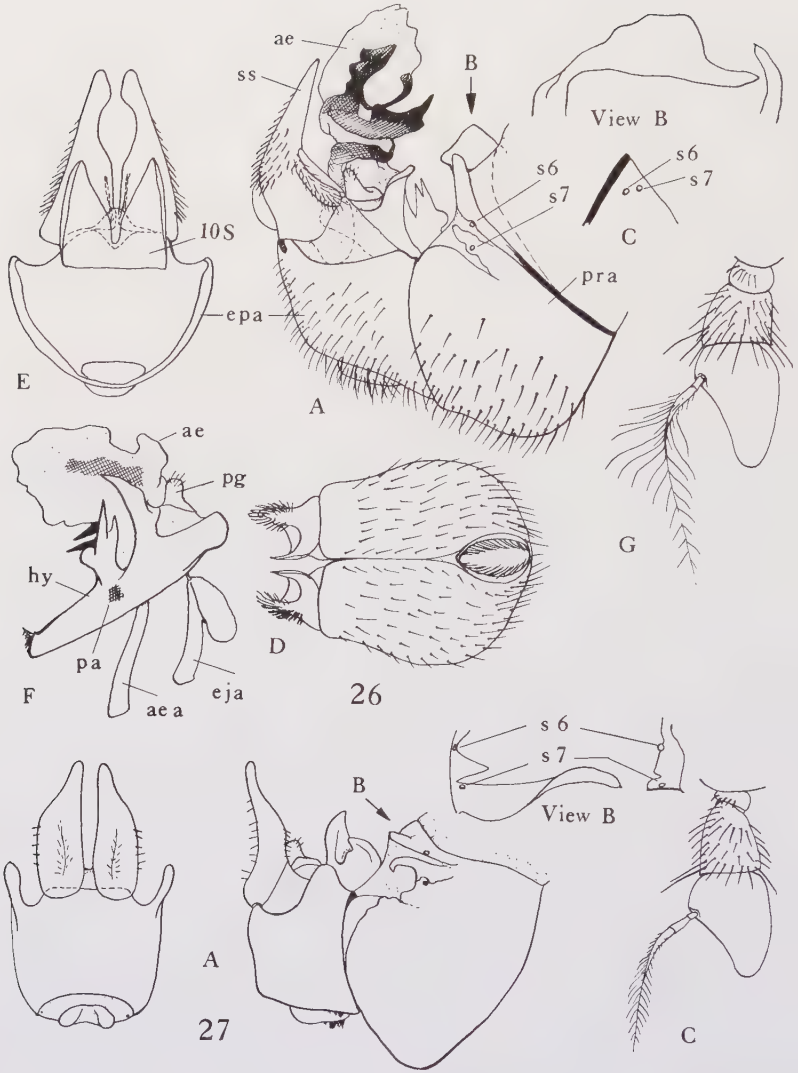
Chaetomacera ferruginea (Fallén) Cresson, 1920, Am. Ent. Soc., Trans., 46: 64.

Tetanocera triangularis Loew, 1861, Berlin. Ent. Zts., 5: 344 (Cent. 1, no. 69); 1862, Monogr. Dipt. No. Am., 1: 122. Not *T. triangularis* auctt., which is a composite of *T. loewi*, *T. mesopora*, and *T. hespera*. *New Synonym.*

Tetanocera huronensis Steyskal, 1938, Mus. Zool. Univ. Mich. Occas. Pap., 386: 6; Ouellet, 1941, Le Nat. Canadien, 68: 135. Syn. by Steyskal, 1954.

Melander did not have North American specimens of this species, and Cresson recorded a few, from Britannia, Ontario, and Ithaca, New York. I have seen a few European examples and find the species fairly common in our fauna from the following localities:

Alaska (Anchorage; King Salmon, Naknek River; Matanuska Valley); British Columbia (Agassiz; Atlin), Saskatchewan (Hays), Manitoba (North Red River; Minnedosa), Ontario (Brittania; Brockville; Bruce Peninsula; English River; Lobo; Marmora; Ottawa; Toronto), Quebec (Cap Rouge; Carillon; Quebec; Rigaud), Oregon (Eagle Ridge, Klamath Lake), Colorado (Boulder), North Dakota (Devil's Lake), South Dakota (Canton; Spearfish; Waubay), Wisconsin (Madison; Dane and Washburn Cos.), Illinois (Cary), Michigan (throughout, including Isle Royale), New York (Albion; Ithaca; Manitou Beach), New Jersey (Newark, salt meadows).



Postabdomens and Antennae of *Tetanocera* Species, Male

FIG. 26. *Tetanocera ferruginea* Fall., Matanuska Valley, Alaska: *A*, left-hand view of extended postabdomen; *B*, ventral view of protandrial sternite; *C*, right corner of protandrium; *D*, posterior view of epandrium and surstyli; *E*, anterior view of epandrium with inner copulatory apparatus removed; *F*, inner copulatory apparatus, right-hand view; *G*, antenna.

24. *Tetanocera bergi* Steyskal

(Figs. 27, 38)

1954, Ent. Soc. Washington, Proc., 56: 66.

I described this species from a few specimens from Matanuska Valley and Auke Bay, Alaska. I have since had the opportunity of examining a good series (v.i.) and can amplify the original description. The surstyli of this form appear to be rather soft; consequently the figure of them in the description, made from relaxed and redried material, is misleading. The angulate profile of the protandrium and the squarish corner of the epandrium to be seen in both figures is very characteristic, as is also the very short aristal plumosity. Sternites 4 and 5 of the preabdomen are divided mesally into two parts; the former has on each half a well-developed setose papilla.

Besides the Alaskan type material, I have seen material from British Columbia (Mission City), Alberta (Banff Nat. Park), and Manitoba (Churchill; mile 505, Hudsons Bay Railway).

25. *Tetanocera plebeia* Loew

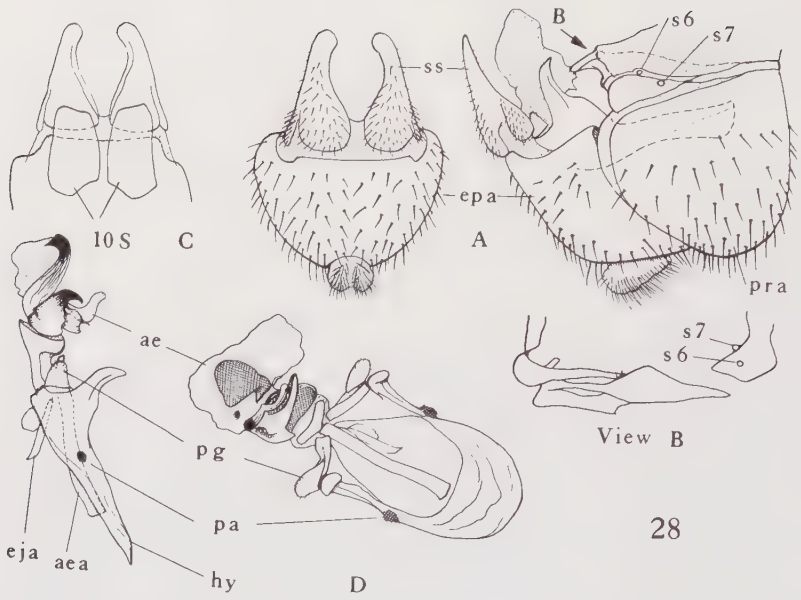
(Figs. 28, 35)

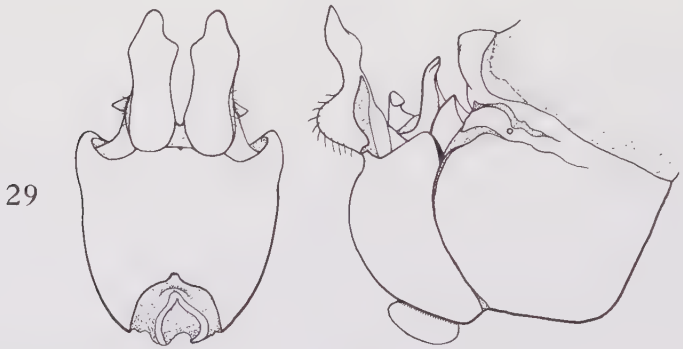
1862, Monogr. Dipt. No. Am., 1: 120; Aldrich, 1905, Smithsonian Misc. Coll., 46: (Cat. No. Am. Dipt.): 579; Hine, 1904, Canadian Ent., 36: 92; 1909, in Adams, Mich. St. Bd. Geol. Surv., Rept. for 1908: 316; Smith, 1910, New Jersey St. Mus., Ann. Rept. for 1909: 797; Young, 1910, New York St. Mus., Rept., 63: 124; Van Duzee, 1911, Canadian Ent., 43: 243; Melander, 1920, Ent. Soc. Am., Ann., 13: 326; Britton, 1920, Connecticut Geol. Nat. Hist. Surv., Bull., 31: 201; Malloch and McAtee, 1923, Ent. News, 34: 233; Johnson, 1925, Boston Soc. Nat. Hist., Occas. Pap., 7: 252; 1927, Biol. Surv. Mt. Desert Reg., pt. 1: 215; Leonard, 1928, Cornell Univ. Agric. Exper. Sta. Mem., 101: 847; Johnson, 1930, Nantucket Maria Mitchell Assn., Publ., 3: 149; Petch and Maltais, 1932, Quebec Soc. Prot. Plants, 29th Rept., suppl.: 67; Brimley, 1938, Ins. No. Carolina: 379; Jaques, 1939, Iowa Acad. Sci., Proc., 45: 283; Knowlton, Harmston, and Stains, 1939, Utah Agric. Exper. Sta., Mimeogr. Ser., 200 (Tech.), pt. 5: 13; Strickland, 1946, Canadian Jour. Res., 24 (D): 168; Steyskal, 1954, Ent. Soc. Washington, Proc., 56: 68.

Chaetomacera elata var. *plebeia* (Loew) Cresson, 1920, Am. Ent. Soc., Trans., 46: 61.

Fig. 27. *T. bergi* Stey., Fort Churchill, Man.: *A*, extended postabdomen; *B*, ventral view of protandrial sternite; *C*, antenna.

Legend: ae—aedeagus; aea—aedeagal apodeme; eja—ejaculatory apodeme; epa—epandrium; hy—hypandrium; pa—point of attachment of hypandrium to epandrium; pg—postgonite; pra—protandrium; ss—surstylus; s6, s7—spiracles of 6th and 7th somites; 10 S—10th sternite.





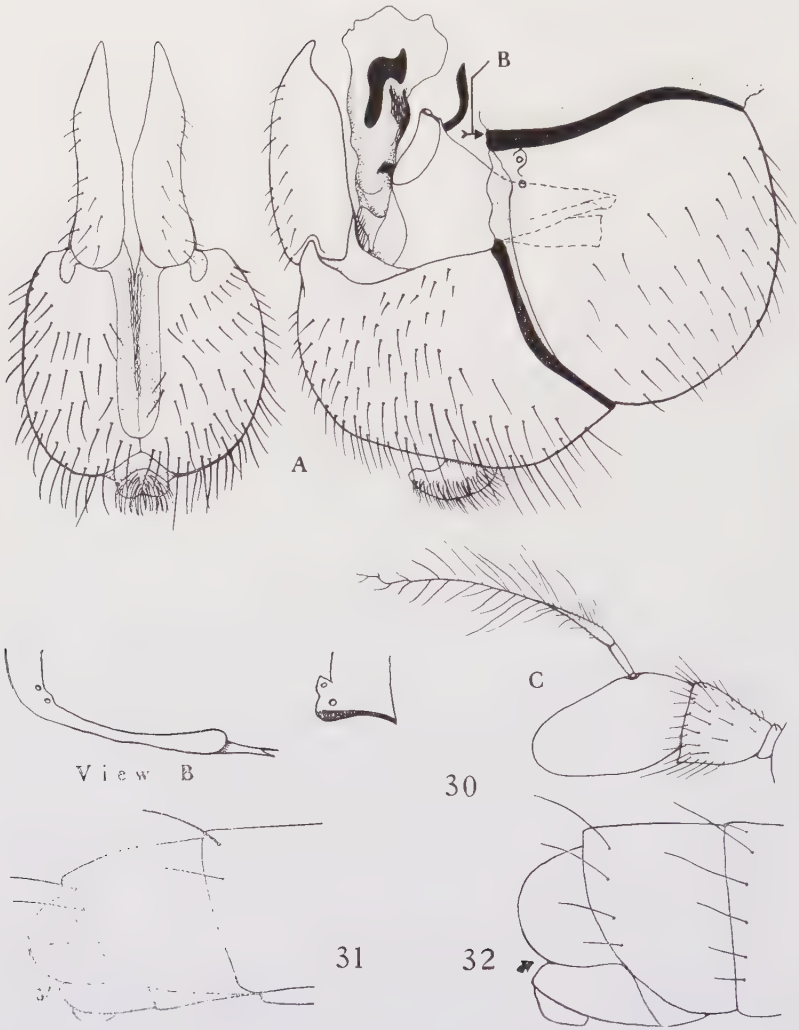
Postabdomens of *Tetanocera* Species, Male

Fig. 28. *Tetanocera plebeia* Lw., Grosse Ile, Mich.: *A*, extended postabdomen; *B*, ventral view of protandrial sternite; *C*, anterior view of tip of epandrium with inner copulatory apparatus removed; *D*, lateral and lateroventral views of inner copulatory apparatus. Legend as in Fig. 26.

Fig. 29. *T. silvatica* Mg., Matanuska Valley, Alaska.

Loew named this species aptly—it is our most abundant and widespread form. The broad and shining interfrontal and parafrontal stripes make it easily recognized after a little acquaintance with it. Furthermore it is the only species in which the female has a shining face. The closed abdomen of a fresh male specimen is shown in Figure 35. I have seen material from the following places:

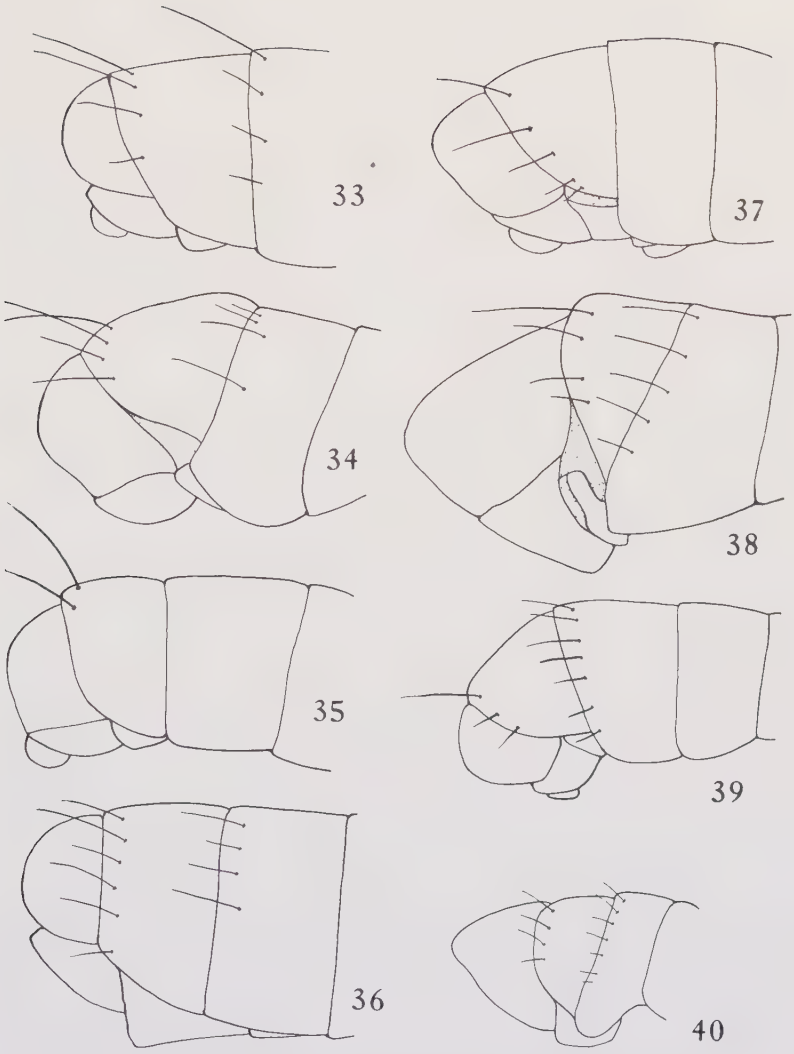
Alaska (Anchorage; Eagle River; Goose Bay; King Salmon, Naknek River; Matanuska Valley; Nebesna; Nushagak), Yukon Territory (Rampart House); British Columbia (Agassiz; Atlin; Carbonate, Columbia River; Coldstream; Colebrook; Jesmond; Jordan River; Salmon Arm); Alberta (Banff Nat. Park, Dapp; Edmonton; Lethbridge; Nordegg), Manitoba (Aweme; Codry V.; Fort Churchill), Ontario (Arnprior; Britannia; Larder Lake; Lake Abitibi; Marmora; Maynooth; Niagara Glen; Normandale; Orillia; Ottawa; Pt. Pelee; Rondeau Park, Kent Co.; Sand Lake; Strathroy), Quebec (Aylmer; Abbotsford; Cap Rouge; Covey Hill; Hull; Joliette; Fort Coulonge; Kazabazua; Knowlton; Laniel; Lanoraie; Meach Lake; Rigaud), New Brunswick (Barber; R. Gornis; Gornish; Youghall), Nova Scotia (Kentville), Labrador (Cartwright), Washington (North Bend, King Co.; Mt. Constitution; Seattle; Yakima), California (Smith River), Utah (Greendale; Logan; Manila; Riverdale; Vernal), Wyoming (Hoback, Teton Co., 6,500 ft.; Yellowstone Park), Colorado (Fort Collins; Rio Branco Co.), New Mexico (Jemez Mts., Jemez Springs), South Dakota (Custer St. Park; Erwin), Minnesota (Duluth), Iowa (Ames; Iowa City; Dickinson, Henry, and Wapello Cos.), Wisconsin (Algoma; Beaver Dam; Columbus; Lake Geneva; Madison; Rhinelander; Waterloo; Dane, Door, and Washburn Cos.), Illinois (Antioch; Channel Lake; Fourth Lake; Fox Lake; Sand Lake; Starved Rock; White Heath), Michigan (throughout, including Isle Royale), Indiana (Lafayette), Ohio (Columbus; Perry and Fairfield Cos.), New York (Aurora; Canton; Elmira; Ithaca; Mt. Hurricane, Essex Co.; Pelham; Rochester; Van Cortlandt; Whiteface Mt.), New Jersey (Forest Hill; Hemlock Falls; Riverton; Winonah), Pennsylvania (Hazleton; Pocono Lake; Roxborough; Delaware and Montgomery Cos.), Maryland (Chevy Chase), West Virginia (Jefferson Nat. Forest), North Carolina (Raleigh; Pineola), Connecticut (Danbury; Lyme), Massachusetts (N. Andover), New Hampshire (Crawford Notch; Mt. Washington).



Details of *Tetanocera* Species, Male

Fig. 30. *Tetanocera stricklandi*, sp. nov., holotype, Nordegg, Alta.: *A*, extended postabdomen; *B*, ventral view of protandrial sternite; *C*, antenna.

Figs. 31–32. Apical half of closed abdomen with only major bristles shown; angular point of juncture of protandrium and epandrium indicated by arrow; drawn from fresh specimens: 31. *T. vicina* Macq., Grand Traverse Co., Mich.; 32. *T. nanciae* Brim., Grand Traverse Co., Mich. (*T. loewi* Steys., sp. nov., is the same).



Apical Half of Abdomen of *Tetanocera* Species, Male

Fig. 33. *Tetanocera montana* Day, Alpena, Mich. (fresh).
Fig. 34. *T. melanostigma*, sp. nov., Grand Traverse Co., Mich. (fresh).
Fig. 35. *T. plebeia*, Lw., Grand Traverse Co., Mich. (fresh).
Fig. 36. *T. mallochi*, sp. nov., Fort Churchill, Man. (dried).
Fig. 37. *T. ferruginea* Fall., Empire, Mich. (fresh).
Fig. 38. *T. bergi* Stey., Fort Churchill, Man. (dried).
Fig. 39. *T. unicolor* Lw., Keweenaw Co., Mich. (fresh).
Fig. 40. *T. spirifera* Mel., Fort Churchill, Man. (dried).

26. *Tetanocera silvatica* Meigen

(Fig. 29)

1830, Syst. Beschr., 6: 41; Hendel, 1900, Zool.-bot. Ges. Wien, Verhandl., 50: 336; 1903, Zts. Hymen. Dipt., 1: 36; Frey, 1924, Notulae Ent., 4: 53; Melander, 1920, Ent. Soc. Am., Ann., 13: 326; Séguy, 1934, Faune de France, 28: 280; Sack, 1939, in Lindner, Die Fliegen d. pal. Reg., 5 (fasc. 37): 54; Verbeke, 1948, Mus. Roy. Hist. Nat. Belg., Bull., 24: 21; Mayer, 1953, Naturhist. Mus. Wien, Ann., 59: 207; Steyskal, 1954, Ent. Soc. Washington, Proc., 56: 69.

Chaetomacera silvatica (Meigen) Cresson, 1920, Am. Ent. Soc., Trans., 46: 65.

The only previous North American record is by Cresson of a specimen from Aweme, Manitoba. The inflated, shining anterior margin of the front makes this species unmistakable in North America. The apical lobes of the surstylus (Fig. 29) are subject to variation. I have seen material from the following localities:

Alaska (Anchorage; King Salmon, Naknek River; Matanuska Valley; Palmer; Tanana), British Columbia (Atlin), Alberta (Banff Nat. Park; Gull Lake), Manitoba (Aweme; Churchill; mile 505, Hudsons Bay Railway), Labrador (Cartwright; Goose Bay), South Dakota (Custer).

27. **Tetanocera stricklandi** Steyskal, sp. nov.

(Fig. 30)

Male. Length of wing, 6.4 mm. This species, in some respects rather aberrant, especially in the postabdomen, is well defined by the key and figures. The wings are yellowish, with but very little browning near tip and with some infuscation about the crossveins. Crossvein *tp* is very straight. There are no stump-veins. The membranous strip between the anal structures and the base of the surstyli, on the meson, is found in no other species.

Holotype, Nordegg, Alberta, July 27, 1936 (E. H. Strickland), in my collection.

SPECIES INQUIRENDAE, NAMES IN SYNONYMY, ETC.

T. acuticornis Van der Wulp, 1897, Biol. Centr. Am., Dipt., 2: 358—Mexico. This is probably a *Hoplodictya*.

T. brevis Cresson (Chaetomacera), 1920, Am. Ent. Soc., Trans., 46: 58. Referred to *Renocera* by Melander.

T. elata Fabricius—a common European form that has been recorded from North America a few times. Cresson considered a few of our species varieties of it. European specimens I have examined are like nothing I have seen from America.

T. flavipes Loew (Gibson, 1917, Ent. Soc. Ontario, Ann. Rept., 47: 157) is a lapsus.
T. huronensis Steyskal. See *ferruginea.*
T. inopa Adams, 1904. Referred to *Limnia* by Melander.
T. papillifera Melander. See *robusta.*
T. parvipyga Malloch (Jaques, 1939) is a manuscript name.
T. pectoralis Walker, 1858, Ent. Soc. (London), Trans., n.s., 5: 321—Mexico. Type examination is necessary to identify this species.
T. phyllophora Melander. See *nigricosta.*
T. plumifera Van der Wulp, 1897, Biol. Centr. Am., Dipt., 2: 359—Mexico. The description is inadequate; type examination is necessary to identify this species also.
T. plumosa Loew, 1847, Stettiner Ent. Ztg., 8: 201—Sitka, Alaska. See *nanciae.*
T. straminata Van der Wulp, 1897, Biol. Centr. Am., Dipt., 2: 357—Mexico. This may not be a *Tetanocera*; the description is insufficient but the figures may permit identification when material becomes available.
T. struthio Walker, 1849, List Dipt. Brit. Mus., 4: 1086—Martin Falls, Canada. The type must be examined.
T. triangularis Loew. See *ferruginea.*

Over the last twenty years a great many friends have given help freely, without which this paper would not have been possible. I wish to express my deep appreciation for their help without mentioning the many names. However, John R. Malloch, Curtis W. Sabrosky, and Guy E. Shewell have contributed so largely that special thanks are due to them.

Papers of the Michigan Academy of Science, Arts, and Letters
Vol. XLIV, 1959 (1958 Meeting)

EXPERIMENTS UPON THE FOOD CONSUMPTION OF THE GRASSHOPPER *MELANOPLUS S. SCUDDERI* (UHLER)

S. K. GANGWERE
*Wayne State University**

It is reasonable that an increase in the size of insects of a given species should require a corresponding increase in the food consumption of the individuals of that species. Relatively few quantitative studies have dealt with the food consumption of Orthoptera, although Roth (1917) has shown that increased food consumption does correlate directly with increased size during nymphal development. Mature female orthopterans are commonly much larger and sometimes twice as large as mature males of the same species, and they are also much less active than males. On the basis of larger size one would predict more food consumption; but on the basis of lesser activity, less food consumption. The analysis of the relative parts played by these two opposing tendencies could doubtless be worked out on certain orthopteran species in which there is both differential size and differential activity in the two sexes.

My experiments were designed to show the relative amounts of foods consumed by adult males and females of a cyrtacanthacridine grasshopper, *Melanoplus s. scudderi* (Uhler). This paper, based upon these experiments, serves to confirm and to extend conclusions from Nagy's more detailed investigation (1952), which utilized a different technique and treated two species belonging to a different subfamily of grasshoppers.

Methods

I selected the short-winged cyrtacanthacridine grasshopper *Melanoplus s. scudderi* for the experiments because the two sexes are markedly different in size and because it is small, easily maintained in the laboratory, and readily obtained near Ann Arbor. I used groups of twenty-one individuals in some tests and twenty-

* Contribution No. 19 from the Department of Biology, Wayne State University, Detroit 2, Michigan.

TABLE I

Results of Test of Food Consumption of Melanoplus s. scudderi (Uhler)

	Food Used	Sex of Feeders	Average Temp. (°F.)	Average Rel. Humidity (%)	Leaf Area Eaten by Group in Two Hours (sq. in.)	Average Leaf Area Eaten by One Feeder in One Hour (sq. in.)	Average Leaf Area Eaten per Gram Mass Feeder in One Hour (sq. in.)
Experiment I	Dactylis	♂♂	89.7	38.3	3.50	0.080	0.348
Experiment I′	Dactylis	♀♀	89.7	38.3	3.62	0.082	0.174
Experiment II	Taraxacum	♂♂	87.3	32.7	4.25	0.097	0.422
Experiment II′	Taraxacum	♀♀	87.3	32.7	5.75	0.131	0.279
Experiment III	Taraxacum	♂♂	85.3	50.7	3.50	0.080	0.348
Experiment III′	Taraxacum	♀♀	85.3	50.7	5.25	0.125	0.268

two, in others, putting these groups in two adjacent cages in the laboratory—males in one, females in the other—where light, temperature, and humidity conditions were the same. Temperature and relative humidity measurements were made with a Serdex thermometer and a Serdex psychrometer. Hunger of all test animals was assured by depriving them of food from 5:00 P.M. of the day before the test until the beginning of the test at 9:30 A.M. the next morning. Each experiment was conducted during the two hours from 9:30 to 11:30 A.M., a period when feeding by this species is normally at a maximum.

During the test periods the males and females were allowed to feed upon the same number of uniform-sized leaves placed in water-filled vials within the two cages. I chose two food plants to represent contrasting food types commonly eaten by orthopterans, selecting ones both measurable and acceptable as foods. These were (1) the exceptionally wide leaves of the coarse grass *Dactylis* and (2)

the large, relatively undissected or entire leaves of the dandelion (*Taraxacum*). Each leaf was first marked with India ink for identification and its outline carefully traced on graph paper. After the two-hour exposure to feeding by the grasshoppers, the uneaten parts of the leaves were immediately superimposed over the drawings of their former outlines, and the consumption in each cage was determined by the total reduction in area of its leaves.

Immediately after the last test the grasshoppers were killed and weighed by beam balance, all the males together and all the females together; the average weight per male and per female was then calculated.

Results

The data from the experiments are tabulated in Table I. The average leaf area eaten per gram mass of body weight in one hour was calculated by dividing the average leaf area eaten by a male or female grasshopper in one hour by its average weight (0.23 grams for males, 0.47 grams for females).

Discussion

In each of these tests the female group ate more than the male group, but this disparity in consumption was small. In fact, when food consumption of the two groups is related to size of feeder, the males are found to eat much more than the females, as expected, for the females have much less surface area per unit of volume than the males, being morphologically and physiologically adapted for egg production; hence, they are less active and need less food. Gross consumption in both groups fluctuated, as expected, with changes in conditions of light, temperature, and humidity. During these studies, attempts were made to measure the temperature and relative humidity, but resulted in data insufficient to warrant further discussion. Measurements of these factors, however, have been made by others, including Parker (1930), who found that food consumption of both nymphs and adults of *Melanoplus m. mexicanus* increased as the temperature rose from 27° to 37° C.

Differences in the ratios of consumption of the two food plants used, as seen in Table I, are possibly interpretable on the basis of greater error in measurement of the narrow grass leaves, the insects' greater difficulty in grasping these blades, and their lesser preference

for this food than for *Taraxacum.** Some minor experimental error may also have resulted from differences in leaf thickness and from wilting.

Roth's findings (1917) suggest that there is a direct positive correlation between size of feeder and food consumption. He found that the nymphs of the phasmid *Carausius* not only increased but actually doubled their food consumption in each successive stadium. Nagy (1952), who worked upon the two oedipodine grasshoppers *Dociostaurus crucigerus brevicollis* and *Oedipoda coerulescens*, found the same sex differential in food consumption as reported here, even though he used a different technique in calculating consumption and worked with a different subfamily of grasshoppers. He did not, however, clearly relate this disparity to activity.

Summary and Conclusions

Food consumption in Orthoptera increases in direct proportion to size during the nymphal stages. In adults, however, this direct relationship between size and food consumption does not appear except perhaps among different-sized individuals of the same sex. While females of a species eat more than males, they eat less per unit of weight, as would be expected from their lesser activity and lower metabolic rate. The consumption ratio between male and female is relatively constant even under fluctuating environmental conditions, for changes in temperature and humidity alter gross consumption without affecting the ratio.

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Nagy, B. 1952. Food Consumption of *Dociostaurus crucigerus brevicollis* Eversm. and *Oedipoda coerulescens* L. Acta Biol. Acad. Sci. Hungar., 3: 41–52.

Parker, J. R. 1930. Some Effects of Temperature and Moisture upon *Melanoplus mexicanus mexicanus* Saussure and *Camnula pellucida* Scudder. Univ. Mont. Agric. Exp. Sta., Bull., 223: 132.

Roth, H. L. 1917. Observations on the Growth and Habits of the Stick Insect, *Carausius morosus* Br. Trans. Ent. Soc. London, III–IV: 345–386.

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* My studies (yet unpublished) have shown that *Melanoplus s. scudderi* prefers *Taraxacum* to *Dactylis*.

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A COMPARATIVE STUDY OF THE STANDING CROPS OF THE MAT-EDGE FAUNA OF THREE BOG LAKES

CLYDE H. ERIKSEN
University of Michigan

Introduction

A bog lake is not a completely definable entity. In attempts at definition, chemical and physical properties have been ascribed, usually with little mention of the biological factors involved except for such all-inclusive statements as that bogs are low in biological productivity. Welch (1936), for example, states that "a bottom fauna is wholly absent save for the possible occurrence of a few microscopic forms in the very tenuous upper portion of the false bottom.... Thus this lake lacks one of the most influential productivity features. Production in this lake thus depends almost wholly upon the biota of the open water and upon the limited marginal population." Jewell and Brown (1929) and Welch (1936) have printed lists of invertebrate animals taken from bogs which have given previous indications of organisms present. Consequently, I made the effort during July and part of August, 1956, to determine accurately, by quantity and quality, some biological features, especially the standing crop, of three bog lakes in the region of Douglas Lake, Cheboygan and Emmet counties, Michigan.[1]

Methods

I selected three "typical" bog lakes, all with an area of open water of low pH surrounded by a floating marginal mat of *Sphagnum*, *Chamaedaphne*, and other bog plants and a flocculent "false bottom" suspended or merging gently into the "true bottom" (Gates, 1942; Welch, 1936, 1952): (1) Bryant's Bog (Silver Lake), near the southwest end of Douglas Lake; (2) Livingston Bog Lake, a little larger than Bryant's and apparently with similar conditions, situated near

[1] I am especially indebted to Mrs. Donald M. Wootton for many hours of help in sorting collections as they came from the field, to Dr. Charles F. Walker for classification of Amphibia, and to Dr. David C. Chandler for guidance and criticism.

Nichols Bog southeast of Douglas Lake; and (3) a larger unnamed bog lake ("Hard Bottom Bog Lake") near Stutsmansville (west of Brutus). Hard Bottom Bog Lake differs from the other two as to mat margin (see Areas), as to false bottom, which is less than two feet deep with a hard (apparently sand) bottom beneath, and as to pH, which measures a low 4.2.

As this is primarily a biological problem, I recorded relatively few physicochemical features: those measured were oxygen, alkalinity, pH, and temperature. I took samples the first two weeks and then every other week thereafter, collecting faunal samples at the mat edge only. Bottom samples were taken at the margin with an Ekman dredge. Plankton was collected, and the mat edge itself can be sampled with a water net of a measured area of 85 cm^2. Five sweeps of approximately 1 m. in length were made at each of six stations around each bog. The number of animals per unit volume was found by dividing the total number of animals by the volume sampled. Volume sampled is equal to the area of the net, times the length of sweeps, multiplied by the number of sweeps. Water samples for all measurements were also taken at the mat edge. pH was measured with a Beckman pH meter. All field work was done on the water from a small aluminum boat. Forms were separated in white trays for classification and tabulation.

Areas

As is true in other lakes, in a bog lake the greater the shore line (littoral zone) as compared to the volume of the lake, the greater is the production of animal numbers. Even though the water is a tea or coffee color, it is so shallow that the bottom is potentially within the photosynthetic zone. Due to the flocculent nature of the bottom, however, it is ruled out as an area of primary production. This leaves phytoplankters and the mat-edge flora to produce organic material on which the complex food webs of the bog organisms depend. Sometimes much algal scum covered the water at Bryant's and Livingston; otherwise plankton was concentrated at mat edge. It is here that the greater part of production results, the quantity largely determined by the type of mat edge. With these ideas in mind, the mat edges of these three bogs will be considered.

Typically, on Bryant's Bog, *Chamaedaphne*, sedges, grasses, and *Sphagnum* complexly interweave in their growth to the water's

edge, with little lopping over onto the water by the *Chamaedaphne*. In some spots, water covers roots, *Sphagnum*, and parts of the stems of the grasses, leaving shallow water in and over these open areas of grass and sedge. The increased surface area afforded by these smaller green plants, compared to relatively little surface area by the larger and woody interwoven stems of *Chamaedaphne*, offers abundant microhabitats suitable for life and production of faunal numbers.

The mat of Livingston Bog Lake has great quantities of woody-stemmed *Chamaedaphne* lopping over onto the water to form an area three to six feet wide from the more solid edge of the mat where the grasses, sedges, and *Sphagnum* grow.

The third lake in question, Hard Bottom (near Stutsmansville), is entirely different. The mat is typically quaking, predominately *Sphagnum*, with comparatively few sedges and little *Chamaedaphne*, which is low and does not lop over into the water. The mat is peculiar in that it is quite solid to the water's edge and gently slopes out into the water instead of dropping off to the false bottom at mat edge. This might be explained by the fact that Hard Bottom is a much larger bog, and ice action is more severe in the winter to the extent of pushing up the mat edges and perhaps overriding the mat vegetation. In two places in particular, on the east and southwest sides, vegetation is almost lacking. Here the mat is an intertwined mass of roots and mud. I believe this condition is mainly due to ice on the east side and to the grazing of cattle on the southwest shore. In most reaches along the mat edge, *Utricularia vulgaris* (bladderwort) forms massive beds of vegetation. This condition is entirely unique to Hard Bottom Bog Lake.

In regard to physical properties (Table I) throughout this study period, it is noted that the pH varies little in each particular bog lake—Bryant's with a pH range from 5.4 to 5.65, Livingston, from 5.43 to 5.57, and Hard Bottom, an extremely low pH from 4.15 to 4.2. Temperatures measured about 20° C. and varied but a few degrees in all three waters. An interesting feature throughout the period was the increase in temperature in Bryant's and Hard Bottom and the slight drop in Livingston. Measurements of methyl orange alkalinity were taken, and all three bogs indicated less than 10 ppm.

Dissolved oxygen in the water shows interesting curves. In Bryant's, it went from 4.44 mg/l. to 3.55 to 2.77 and finally to 2.68 mg/l. at the time of the last collection. In Hard Bottom Bog, the

TABLE I

PHYSICOCHEMICAL FEATURES AND BIOLOGICAL PRODUCTIVITY OF BRYANT'S, LIVINGSTON, AND HARD BOTTOM BOGS

Description (at mat edge)	Bryant's				Livingston				Hard Bottom			
	7–3–56	7–11–56	7–24–56	8–7–56	7–4–56	7–11–56	7–24–56	8–2–56	7–4–56	7–10–56	7–25–56	8–8–56
Air temperature	27°C	23.3°C	21.3°C	31.5°C		29°C	29.5°C	21.5°C			27°C	23.5°C
Water temperature (1 foot)	18.5°C	19.5°C	20°C	20°C	21°C	20.5°C	21°C	20°C	no collection	20°C	20.5°C	21°C
Dissolved oxygen (mg./l.)	4.44	3.55	2.77	2.68	4.02	6.16	5.22	3.81		5.68	7.12	6.86
Alkalinity (methyl orange)	8ppm	7ppm	7ppm	6.1ppm	7.3ppm	8.3ppm	8ppm	6.3ppm		9.5ppm	6ppm	5.3ppm
pH	5.61	5.62	5.40	5.65	5.43	5.43	5.57	5.50		4.20	4.15	4.15
Depth	1.75M	....	....	....	1.74M 2.03M	....	....	....		0.6M 1.04M	....	....
BOTTOM FAUNA												
DIPTERA												
Tendipedidae	22	24	26	20	4	1	—	3		14	19	—
PLANKTON												
Tendipedidae	—	—	*	—	—	—	*	—		*	*	*
Culicidae												
Chaoborus sp.	****	*****	***	**	*	—	—	—		—	—	—
Daphnidae												
Daphnia sp.	**	**	**	**	*	*	*	**		***	*	**
Diaptomidae												
Diaptomus sp.	*	**	**	***	*	**	—	—		—	—	—

Hydrachnidae												
Hydrachna sp.	*	*	*	*	—	—	—	—		—	—	—
ROTIFERA												
Keratella taurocephala	*	*	*	*	*	**	—	—		*****	*****	—
PROTOZOA												
Arcella sp.	—	—	—	*	—	—	—	—		*	*	—
Dinobryon sp.	*	*	****	—	—	—	—	—		**	**	—
Euglena sp.	—	—	—	—	—	—	*	—		—	—	—
Paramecium sp.	—	—	—	—	—	—	*	—		—	—	—
MAT EDGE FAUNA												
ODONATA												
Anisoptera												
Leucorrhinia sp.	373	401	337	351	194	378	212	184		279	412	267
Leucorrhinia sp.	40	43	80	68	31	31	53	4		—	—	—
Libellula sp.	164	211	255	217	86	118	100	76		9	—	9
Somatochlora sp.	12	24	31	36	6	10	1	—		1	4	—
Aeschna sp.	2	—	3	3	—	—	—	—		3	16	20
Anax sp.	1	10	11	10	2	2	—	4		—	2	—
Boyeria sp.	—	—	—	—	—	2	3	—		—	—	—
Zygoptera												
Anamalagrion hastatum	1	—	—	18	—	1	58	—		—	6	6
Lestes sp.	24	19	5	1	2	6	—	—		2	1	—
Ischnura sp.	—	—	—	—	—	—	—	131		—	—	8
	76.5%	72.2% (74.8%)	73.5%	77.1%	71.3%	74.3% (72.9%)	73.9%	71.9%		74.8%	80.9% (78.2%)	78.7%
COLEOPTERA												
Dyticidae												
Ilybius sp.	—	L-1	—	—	1	2	1	—		2	—	2
Colymbetes sp.	—	—	1	—	—	—	—	—		—	—	1

TABLE I—(*Continued*)

Description (at mat edge)	Bryant's				Livingston				Hard Bottom			
	7-3-56	7-11-56	7-24-56	8-7-56	7-4-56	7-11-56	7-24-56	8-2-56	7-4-56	7-10-56	7-25-56	8-8-56
COLEOPTERA												
Dyticidae												
Rhantus sp.	—	—	—	2	—	—	—	—		—	1	1
Dytiscus sp.	1	1	—	—	—	—	—	—		—	3	—
Hydaticus sp.	1	—	—	—	—	—	—	—		—	—	—
Acilius semisulcatus	1	3 L-1	5 L-1	5	L-5	1	—	L-1		2	1	7
Bidessus sp.	2	—	2	2	—	—	—	—		—	—	—
Desmopachria sp.	—	—	1	—	—	—	—	—		—	—	—
Hygrotus inequalis	8	16	22	3	—	—	—	1		5	11	5
Hydroporus sp.	L-1	1 L-1	1	1	—	—	—	—		—	—	—
Graphoderus sp.	L-3	1	—	—	3	2	11	5		—	1	—
Copelatus sp.	—	—	—	—	—	1	—	—		—	—	—
Coptotomus sp.	—	—	—	—	—	1	1	—		—	L 2	—
Hydrophilidae												
Hydrochara sp.	—	—	1	—	—	—	—	—		—	—	—
Tropisternus sp.	L-6	L-5	3 L-5	L-3	—	—	L-4	1		L-1	L-2	2
Enochrus sp.	—	—	1	—	—	—	—	—		—	—	—
Paracymus sp.	—	2 L-1	—	—	—	—	—	—		—	—	1
Haliplidae												
Haliplus sp.	9	4	13	1	—	1	—	8		2	5	5
Peltodytes sp.	2	—	4	2	—	1	—	1		2	5	3

COLEOPTERA												
Gyrinidae												
Dineutus sp.	*	*	*	*	*	*	*	L-1*		L-1*	L-1*	*
Gyrinus minutus	—	—	—	—	—	—	—	—		*	*	*
	4.2%	3.8%	6.1%	2.1%	2.0%	1.2%	2.9%	3.2%		3.8%	5.9%	6.9%
	(4.1%)				(2.4%)					(5.5%)		
HEMIPTERA												
Notonectidae												
Notonecta (nymphs-all sp)	9	14	6	8	—	—	—	—		—	—	—
N. borealis	3	3	2	2	—	—	—	2		—	—	—
N. irrorata	—	—	3	3	10 L-13	9 L-25	L-23	4 L-8		—	—	—
N. undulata	1	—	—	—	—	—	—	1		1 L-65	9 L-49	3 L-41
Buenoa sp.	—	1	—	—	16 L-21	1 L-15	L-2	7 L-21		2 L-2	6	6
Nepidae												
Ranatra sp.	1	3	4	—	—	—	—	—		2	1	—
Belastomatidae												
Belastoma sp.	12	23	6	17	1	3	6	7		1	—	—
Lethocerus sp.	—	—	7	4	—	—	2	2		4	—	1
Corixidae												
Trichocorixa sp.	—	—	2	—	—	2	3	3		—	—	—
♀ Corixidae (and immature)	7	20	3	4	15	47	59	32		5	1	—
Hydrometridae												
Hydrometra martini	—	1	—	—	—	—	2	—		—	—	—
Mesoveliidae												
Mesovelia mulsanti		numerous				numerous				numerous		

TABLE I—(*Continued*)

Description (at mat edge)	Bryant's				Livingston				Hard Bottom			
	7–3–56	7–11–56	7–24–56	8–7–56	7–4–56	7–11–56	7–24–56	8–2–56	7–4–56	7–10–56	7–25–56	8–8–56
HEMIPTERA												
Microvelia sp.	numerous				numerous				numerous			
Gerridae												
Gerris sp.	*	*	*	*	*	*	*	*		*	*	*
	4.1%	6.6%	3.4%	4.2%	16.9%	13.8%	16.8%	15.7%		20.9%	12.1%	12.9%
	(4.6%)				(15.8%)					(15.3%)		
TRICHOPTERA												
Leptoceridae												
Triaenodes sp.	4	—	—	2	2	—	1	13		2	2	3
MEGALOPTERA												
Corydalidae												
Chauliodes sp.	—	—	—	—	—	—	—	—		—	L-4	L-3
AMPHIBIA												
Hyla crucifer	40	52	33	9	10	37	9	—		—	—	—
H. versicolor	25	27	10	6	11	5	1	—		—	—	—
Rana clamitans	27	58	119	129	7	34	18	38		—	—	—
Diemyctylus viridescens	2	5	3	4	—	1	3	—		—	—	—
Ambystoma jeffersonianum	2	2	1	2	—	—	—	—		—	—	—
Unidentified specimens	23	27	—	—	14	2	5	—		—	—	—
	14.7%	17.4%	16.9%	16.4%	9.3%	10.7%	6.2%	6.8%		0%	0%	0%
	(16.4%)				(8.3%)					(0%)		

DIPTERA												
Tendipedidae	*****	*****	*****	*****	*	***	*	*		**	*	**
Ceratopogonidae	—	—	—	—	*	*	—	—		*	—	—
Tipulidae	—	—	1	—	—	—	—	—		—	—	—
Culicidae												
Culex sp.	*	*	*	*	*	*	*	—		—	*	*
Chaoborus sp.	*****	*****	*****	*****	*	***	*	—		***	*	*
CLADOCERA												
Daphnia sp.	*	*	*	*	*	*	*	—		—	*	—
HYDRACARINA												
Hydrachna sp.	*	*	*	*	*	—	—	—		—	—	—
Eylais sp.	*	*	*	*	—	—	—	—		—	—	—
Total Numbers	829	1005	1008	933	454	739	578	558		407	564	394
	*28	*30	*33	*28	*15	*19	*12	*7		*23	*19	*12
Total Genera &/or Species	44	41	45	41	31	37	33	28		30	33	28
Mat-Edge Numbers	807	981	982	913	450	738	578	555		393	545	394
Mat-Edge Gen. &/or Species	33	30	33	30	20	27	25	24		20	23	21
Mat-Edge Numbers (without Amphibia)	688	810	816	763	408	659	542	517		393	545	394
Mat-Edge Gen. &/or Species (without Amphibia)	27	24	28	25	16	22	20	23		20	23	21

— indicates absence in collection.

* indicates presence and relative abundance.

L indicates larval or nymphal stage where adults are also aquatic, e.g., 3 L-5 means 3 adult and 5 larval forms.

dissolved oxygen rose from 5.7 mg/l. to 7.12 mg/l. and then dropped to a low of 6.86 mg/l. on the last collection. Similar results were seen at Livingston (4.02 to 6.16 to 5.22 to 3.81 mg/l.). Although the water above the false bottom is shallow in all three bogs, it is noted that the larger Hard Bottom Bog is the shallowest (0.6 to 1.04 m), whereas Livingston is about 2 m. deep and Bryant's, 1.74 m.

Results

In contrast to such previous studies as Welch (1936), macroscopic forms were collected from each false bottom—all dipterans (Tendipedidae). The number of individuals collected in each Ekman dredge sample were consistently higher in Bryant's than in the other two, though in the same respect, Hard Bottom possessed more individuals per unit area than did Livingston. Bryant's Bog Lake had the greatest quantity of plankters. Excluding large quantities of the small rotifer *Keratella*, found in the plankton of Hard Bottom Bog Lake, the plankton of Livingston and Hard Bottom were about equal.

In considering only those forms that harbor in the mat margin, the standing crops of sequential collections show the bell-shaped curve of population growth and decline. The time of attainment of the population peaks in these three bogs is noted to be different (Table I and Fig. 1). The standing crop, as measured by the total number of individuals, is greatest in Bryant's with Livingston far behind and Hard Bottom even less populated. It is seen that the number of genera, or species, or both, is greatest in Bryant's—33, 30, 33, 30;[2] fewer in Livingston—20, 27, 25, 24; and consistently fewer still in Hard Bottom—20, 23, 21. Although a few genera are exclusive to one bog, most forms were generally found.

The total absence of tadpoles in Hard Bottom and the small percentage of Coleoptera in Livingston and Hemiptera in Bryant's is seen in Table I. It is interesting to note the distribution of *Notonecta* species in these bogs. In Bryant's, *N. borealis* and *N. irrorata* are predominant species, and only one specimen of *N. undulata* was taken. But in Livingston, *N. irrorata* is still predominant, and only one specimen of *N. undulata* and two of *N. borealis* were taken. Hard Bottom yielded no *N. borealis* or *N. irrorata*, only *N. undulata*. Odonates are seen to comprise about 75 per cent of the animal fauna

[2] Refers to number of genera or species or both.

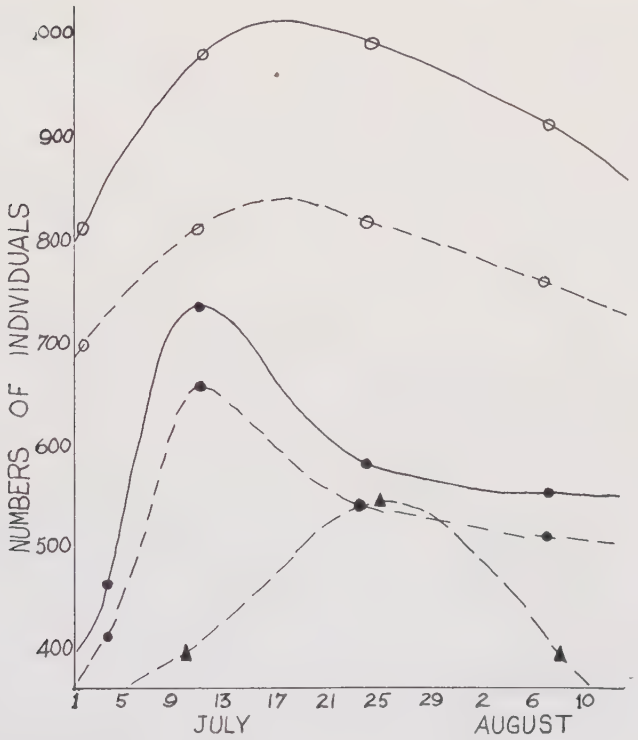

Fig. 1. Population peaks of standing crops.

of these mat margins. In Bryant's and Livingston, tadpoles totaled 16.4 per cent and 8.3 per cent, respectively. In Livingston and Hard Bottom, Hemiptera composed more than 15 per cent of the total population but only 4.6 per cent in Bryant's. Coleoptera was the other significant group, comprising more than 4 per cent in Bryant's and Hard Bottom and 2.4 per cent in Livingston.

Discussion

It is claimed that the biological productivity of bog lakes is very low due to pH, false bottom, and the like (Welch, 1936, 1952). But in view of the conditions and collections of this study, I believe they

indicate that this is not true; rather, upon close examination and study, bog lakes can be shown to be relatively highly populated. No collection was made on the mat, so, as stated, productivity may be recognizably low. Bottom forms in the flocculent false bottom are few but are present in fairly constant numbers as shown by Table I. Plankton is slight if hauls are made in the open water; however, the closer the mat edge of the lake is approached, the more numerous plankton becomes. In this regard, it is well known that with the change from day to night planktonic forms migrate vertically as a response to light. In the studied bog lakes, vertical migration of plankters is extremely limited due to the shallowness of water above the false bottom. Therefore, if under these conditions a migration occurred as a response to light, it would result in the plankters merging into the false bottom or perhaps migrating laterally to the darker reaches of the marginal vegetation. Since planktonic forms were absent from the false bottom, the last suggestion seems the more plausible. Although the actual reason for this condition remains unclear, this concentration of plankton at the mat margin increases the efficiency of a basic unit in the food webs of the teeming life of the mat edge. Although Welch (1936) says the mat edge has a scanty population, I found great numbers of organisms in the mat edge in each of the bogs examined.[3]

While there are other factors, the type of mat edge seems the most important single one in determining organic production. That is, the type of vegetation and its physical arrangement determines, to a large extent at least, the number of organisms that the bog is able to support. For example, Bryant's Bog has shallows along the margin of the mat where grasses and sedges replace the *Chamaedaphne*. Here the surface area for organic production is comparatively high which, in combination with the afforded niches for animal habitation and foraging, results in a relatively large standing crop. The mat edge at Livingston Bog is rather different with a broad zone of only woody-stemmed *Chamaedaphne* over the water. The lack of grasses, sedges, and shallows in the mat margin limits the organic production of this bog lake. One might then expect that, except for the muddy, nonvegetated areas of Hard Bottom Bog, the type of mat edge would yield a greater photosynthetic zone, and thus a greater standing crop. But in most reaches along the

[3] No work was done on stratification of fauna, but it was noted that most organisms were taken from approximately the top foot.

mat edge, *Utricularia vulgaris* forms massive beds of vegetation that "choke out," to a large extent, production in shallows of the marginal mat. Due to its "carnivorous" tendencies on planktonic forms, this unit of basic productivity is decreased and is noticeably low. In addition, the extremely acid nature of the water (pH 4.15 to 4.2) would certainly have an effect on the kinds and numbers of organisms found herein.

Since about 75 per cent of the bog populus is odonates, the general faunal production curves would largely be set by these forms, and this is seen to be true.

Aside from the size and variation in standing crop in each bog lake, Figure 1 shows population peaks at different times. Since genera of organisms found in each bog were comparably similar, developmental time would seem to be similar. But a difference is noted. At first thought this might be correlated with temperature of the water relative to development. Since such shallow depths are usually homothermous, one would expect the deepest to be coldest and therefore show the latest population peak. This is not so; in fact, the reverse is true, but available data does not offer an explanation.

Summary

1. I studied three bog lakes in northern, lower Michigan (near Douglas Lake) for two summer months in 1956.

2. As expected, population numbers varied with each bog, and sequential collections showed the bell-shaped curve of population growth and decline.

3. Odonates comprised about 75 per cent of the animal fauna of the mat margins; tadpoles, hemipterans, and coleopterans comprised the other significant groups.

4. These bogs are exceedingly more productive than previous research would lead one to believe. Production of numbers (as measured by standing crop) is correlated with conditions found. The type and physical arrangement of the mat margin, combined with the concentration of planktonic forms at mat edge, seem the most influential determinants of productivity.

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HERMAPHRODITISM IN SOME SERRANID FISHES FROM BERMUDA*

C. LAVETT SMITH
University of Michigan

Occasional or teratological hermaphrodites are known in many fishes, and at least three families (Maenidae, Sparidae, and Serranidae) are known to include species that are normally hermaphroditic. Maenid and sparid fishes may be either protandrous or proterogynous (D'Ancona, 1950; Aoyama, 1955). The gonad is divided into well-marked male and female parts, and protandry or proterogyny occurs when one zone is active before the other. Thus, the sexes are functionally distinct. According to D'Ancona, rudimentary hermaphroditism may lead to secondary gonochorism (1952).

Some serranid fishes are synchronously hermaphroditic (Van Oordt, 1929; D'Ancona, 1950; Longley and Hildebrand, 1941; Ginsburg, 1952). As in the Sparidae and Maenidae, the gonad is differentiated into testicular and ovarian zones, but the male elements are situated along the cavity of the gonad rather than embedded in the stroma. Both male and female parts are active simultaneously, and for some species autofertilization has been suggested (Dufosse, 1856). It seems likely, however, that some physiological or genetic barriers may prevent self-fertilization under natural conditions. Johnson (1932) indicated the possibility of autofertilization in a teratologically hermaphroditic scup, *Stenotomus chrysops* (Linneaus); perhaps normally gonochoritic species have not developed barriers to self-fertilization.

A third type of sexuality, again in the Serranidae, has been noted by Lavenda (1949). This is a type of proterogyny which stands in stark contrast to that in the sparid and maenid fishes since the ovotestis is not divided into male and female territories but changes

* Contribution No. 237 from the Bermuda Biological Station.

Field work was supported by the Bermuda Fisheries Research Program under the direction of Dr. John E. Bardach and Figures 1 and 2 are reproduced from the final report of this program. Some of the specimens used in this study were collected while the author was a visiting investigator at the Lerner Marine Laboratory of the American Museum of Natural History at Bimini, British West Indies.

in toto. In 6,000 individuals of the black sea bass (*Centropristes striatus* Linnaeus) Lavenda found a higher proportion of males among the larger-sized classes. He explained this on the basis of proterogynous hermaphroditism and was able to support this hypothesis histologically. Van Oordt (1933) had found similar histological patterns in certain Javanese epinepheline serranids, but he did not have large series of field data and therefore failed to recognize these hermaphrodites as transitional stages in proterogynous species.

The Bermuda fauna is rich in serranid fishes, which are being studied under the auspices of the Bermuda fisheries research program. Of the species reported from the islands, at least nine are proterogynous and four are synchronous, functional hermaphrodites.

Methods

I made field studies in Bermuda from June 15 to August 31 in 1956 and from March 15 to June 14 in 1957. Measurements of lengths were taken on specimens in the commercial catch as well as on those collected by the staff of the Bermuda Biological Station. After it was found to be impossible to determine by gross inspection the sex of individuals in the inactive state, sex was recorded as male, female, or inactive. Gonad samples for histological study were prepared according to standard methods and sectioned in paraffin at 10 and 15 μ. A small piece of the gonad was removed, usually from the central part of the right organ, although those of larger individuals were taken more or less randomly from any convenient region. Samples collected in the summer of 1956 were fixed *in situ* in 10 per cent formalin and stained in hematoxylin and eosin. Those collected in 1957 were fixed in Bouin's fluid and stained with the more yolk-specific iron hematoxylin.

Synchronous Hermaphrodites

The four Bermuda species, all members of the subfamily Serraninae, found to be synchronously hermaphroditic are *Hypoplectrus unicolor*, *Prionodes phoebe*, *P. tabacarius*, and *P. tigrinus*. The first two are common in Bermuda waters, and specimens were available for sectioning and dissection. The others are rare in Bermuda, and specimens collected near Miami, Florida, and Bimini, British West Indies, were examined by gross dissection.

The appearance of the ovarian and testicular tissue is quite differ-

ent, and hermaphroditic organs can easily be recognized by their gross appearance; the creamy-white male zone contrasts sharply with the granular ovarian tissue. The male part is much the smaller and lies in the posterior ventral wall of the gonad. The sperm are not released into the lumen as are the eggs but are collected by a separate duct.

Sections of the ovotestes of *Prionodes phoebe* collected during May and July and those of *Hypoplectrus unicolor* collected during late June revealed tailed sperm and ripening eggs in which the *zona radiata* were well developed. It seems certain that these individuals would have spawned as both male and female during the same season and presumably at the same time. The structure of the reproductive organs of these species seems to be the same as that reported by Van Oordt (1929) for three related Mediterranean species.

Proterogynous Species

All of the Bermuda serranids found to be proterogynous are members of the subfamily Epinephelinae, commonly called groupers. These fishes are cosmopolitan in tropical and subtropical marine waters. Sexual dimorphism, except for size, is not well developed and those features that might be interpreted as secondary sex characters (e.g., the exsertion of the dorsal, anal, and caudal soft rays in *Mycteroperca tigris*) can equally well be considered functions of size.

This study includes the following Bermuda species: *Epinephelus guttatus*, *E. striatus*, *Mycteroperca bonaci*, *M. tigris*, *M. falcata*, *M. venenosa*, *Cephalopholis fulvus*, *Petrometopon cruentatus*, *Alphestes afer*, *Promicrops itaiara*, *Paranthias furcifer*, and *Rypticus saponaceus*. All except the last two were proterogynous on the basis of the following evidence: (1) no males were found in the smallest-sized groups, (2) males appeared among medium-sized fish and the proportion increased among the higher-sized classes until the largest-sized groups were exclusively males, and (3) regressive oöcytes were found in the testes of functional males. In all of these species the mechanism seems to be the same, and the description given here is a composite based upon all of the material listed in Table I.

Figures 1 and 2 show the size frequency distribution of the two most common species in the Bermuda commercial catch. Other species, of which fewer individuals were available, show similar patterns. In each species no small males were found, and the pro-

TABLE I

SUMMARY OF HISTOLOGICAL STUDIES ON GONADS OF SERRANIDAE
(Numbers in parentheses indicate range of standard length in millimeters.)

Species	Females	Males*	Total
Epinephelus guttatus (Linnaeus)	80 (114–385)	26 (217–350)	106
Epinephelus striatus (Bloch)	41 (142–417)		41
Mycteroperca tigris (Valenciennes)	23 (155–421)	5 (387–618)	28
Mycteroperca falcata (Poey)	9 (223–321)		9
Mycteroperca bonaci (Poey)	14 (286–515)	7 (1000–1150)	21
Mycteroperca venenosa (Linnaeus)	4 (249–489)		4
Alphestes afer (Bloch)	7 (132–235)	1 (213)	8
Petrometopon cruentatus (Lacepede)	19 (117–246)	3 (203–259)	22
Cephalopholis fulvus (Linnaeus)	23 (112–240)	18 (201–320)	41
Promicrops itaiara (Lichtenstein)		1 (1602)	1
Rypticus saponaceus (Bloch)†	5 (130–263)	1 (263)	6
Paranthias furcifer (Cuvier)†	3 (224–273)	1 (197)	4
Prionodes phoebe (Poey)	Synchronous hermaphrodites		2
Hypoplectrus unicolor (Walbaum)	Synchronous hermaphrodites		2
Total			295

* All specimens in which development of male tissue could be detected are listed as males. The slow retrogression of some oöcytes makes it impractical to distinguish between males and transition stages.

† Data inconclusive; perhaps these two species are gonochoritic.

portion of males increased with increasing size. In the preparation of these graphs only ripe fish and those sexually inactive but for which sex was determined histologically were included.

The ovotestes are paired, sac-like organs lying in the posterior dorsal part of the body cavity. They are broadly joined behind to form the oviduct, which emerges at the tip of the genital papilla. No gross differences between ripe testes and ripe ovaries were found. The capsule of the gonad is composed of several layers of smooth muscle covered externally by the peritoneum. The organ is supported by a mesentery which joins it to the body wall, posteriorly, and to the wall of the gas bladder, anteriorly. The genital artery and vein run within the capsule wall near its juncture with the mesentery and send branches to all parts of the gonad. In this region also lies the glandular material which Lavenda (1949: 192) has suggested

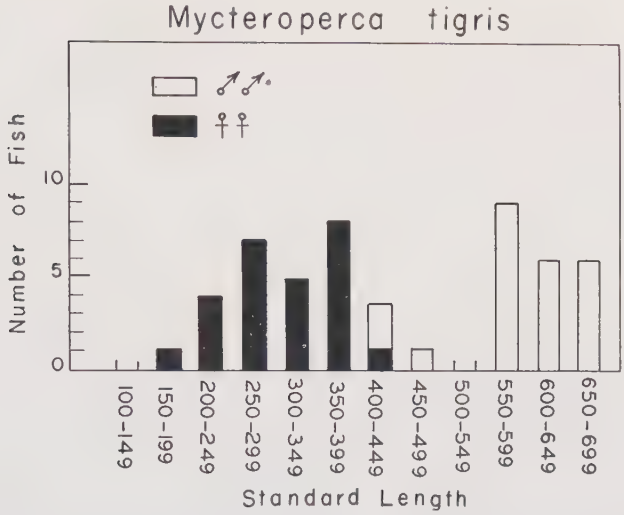

FIG. 1. Size-frequency distribution of the sexes of *Mycteroperca tigris* from Bermuda. (Courtesy of Bermuda Fisheries Research Program, Dr. John E. Bardach, Director.)

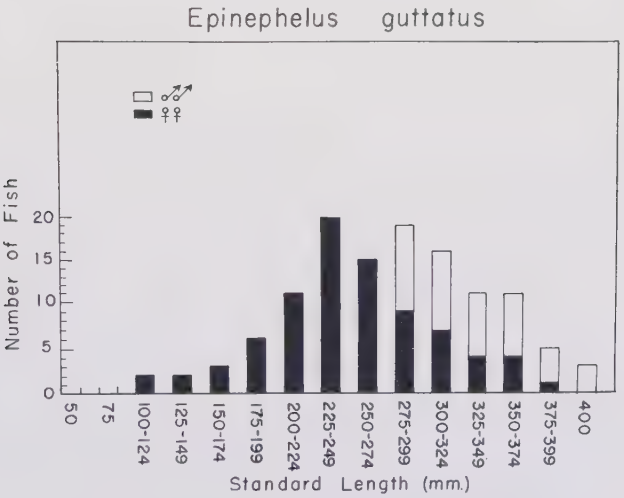

FIG. 2. Size-frequency distribution of the sexes of *Epinephelus guttatus* from Bermuda. (Courtesy of Bermuda Fisheries Research Program, Dr. John E. Bardach, Director.)

may be medullary adrenal tissue. This chromophilic, apparently endocrine, tissue is present in both males and females, but it does not run through the entire length of the gonad, appearing only in sections cut from the posterior part of the organ. I have not seen it in the synchronously hermaphroditic species.

Extending into the lumen of the ovotestis are many lamellae of varying sizes. These are slightly oblique to the axis and thus have a somewhat spiral form. The ventral medial wall bears no lamellae, and the resulting space apparently serves as a passage for sex products produced in the anterior part of the organ. Lamellae end where the right and left organs join, leaving the wall of the oviduct without germinal tissue.

Each lamella consists of a central wall of smooth muscle, capillaries, and connective tissue surrounded by a spongy layer of connective tissue matrix supporting the germinal and other cells. In immature gonads cells appearing to be primary oöcytes lie along the outer wall of the lamella embedded in a dense mass of smaller cells. As the female stage develops, more oöcytes are formed and the other cells become much less prominent (Fig. 3). Very young oöcytes are nearly uniform in texture and stain dark with hematoxylin. As they mature the central nucleus becomes clear, with dark-staining chromatin granules around its periphery. Later the cytoplasm becomes filled with oil droplets (appearing as vacuoles in sectioned material) and very heavily stained yolk platelets. Iron hematoxylin stains the yolk granules nearly black, and thus they can be recognized even after they have been withdrawn into the follicle cells during postspawning degeneration. As the yolk granules are forming, the membranes develop and the *zona radiata* becomes particularly conspicuous. The developing ova are formed within thin-walled follicles held in place by reticular fibers. Also seen at this stage are groups of small, lightly staining cells, some of which are destined to give rise to the seminiferous crypts of the male phase. Not all of the ripe ova are released during spawning, and afterward these and many early-stage oöcytes remain, but no *corpora lutea* were seen during this study. During the transitional stages (Figs. 4–5) the remaining female cells begin to degenerate. The early stage oöcytes are reabsorbed rapidly, but the later stages regress slowly, and even the oldest males usually have some trace of degenerating oöcytes. In the breakdown the cell contents including the yolk platelets are

withdrawn into the follicle cells, leaving the egg membranes collapsed (Figs. 6–7). Finally these disappear and for a time only the yolk platelets within the follicle cells remain. During the inactive period the seminiferous crypts develop and active spermatogenesis begins before the next breeding season (Fig. 8).

The factors triggering the transition are not known, but the size range of the females of some species (particularly *Epinephelus striatus*) indicates that more than one spawning season is passed in the female phase.

Discussion

Within the family Serranidae three types of sexuality are known. Freshwater species (genus *Roccus*) are gonochoritic, and the only known hermaphrodites are teratological (Schultz, 1930). Most species of the subfamily Serraninae are synchronously hermaphroditic, but the black sea bass of the Atlantic coast, which seems properly placed in the subfamily, has been shown to be proterogynous. All members of the Epinephelinae so far studied seem to be proterogynous, although the divergent *Paranthias furcifer*, provisionally placed in this subfamily, may be gonochoritic (Table I). Data are inconclusive for *Rypticus saponaceus* (subfamily Grammistinae), but it too may be gonochoritic.

Although some members are highly specialized, the Serraninae, in my opinion, are closest to the ancestoral serranid stock. It seems most likely that proterogyny has been derived from synchronous hermaphroditism. Whether the gonochorism of the other subfamilies has likewise been secondarily derived from hermaphroditic ancestors cannot be answered at present.

It is not known what factors trigger the change from female to male, but an investigation of this problem could begin with a study of the glandular tissue lying in the region of the genital veins.

The size dimorphism between the sexes may prove of value in future management practices because the catch could, by appropriate size restrictions, be limited to either sex or to any proportion of the sexes. If it is found that a single large male can service several females, proportionately more males could be harvested.

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PLATE I

Sections of ovotestes showing typical stages in the change from female to male.

Fig. 3. Cross section through a portion of the gonad of a specimen of *Cephalopholis fulvus*, 183 mm. in standard length, showing the structure of the lamellae during the female phase.

Fig. 4. Cross section of the gonad of a specimen of *Cephalopholis fulvus*, 239 mm. long, in the transitional stage, showing developing seminiferous crypts and young oöcytes not yet reabsorbed. Spermatogenesis not yet evident.

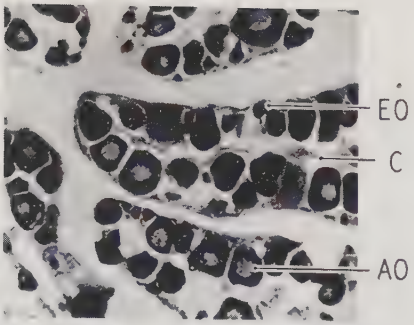
Fig. 5. Cross section through the gonad of *Cephalopholis fulvus*, 256 mm. long. Some oöcytes remain, but there is active spermatogenesis in the seminiferous crypts.

Fig. 6. Cross section through the gonad of a specimen of *Epinephelus guttatus*, 350 mm. long. Inactive male phase. Early oöcytes have disappeared, but the later stages are still being reabsorbed.

Fig. 7. Same individual as Fig. 6. High power view of degenerating ova showing collapsed egg membranes and follicle cells containing yolk platelets which have been withdrawn from an advanced ovum.

Fig. 8. Cross section through the gonad of a male *Mycteroperca bonaci* 1050 mm. long. Mature male phase showing remnants of an ovum.

Abbreviations.—EO, early oöcyte; AO, advanced oöcyte; C, central wall of lamella; O, oöcyte; S, seminiferous crypt; FC, follicle cells; M, collapsed egg membranes.



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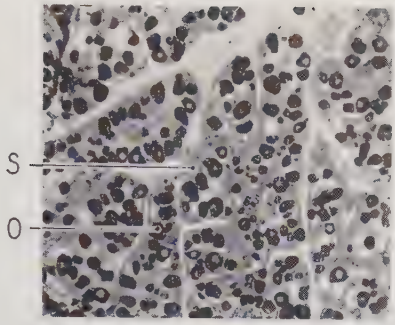

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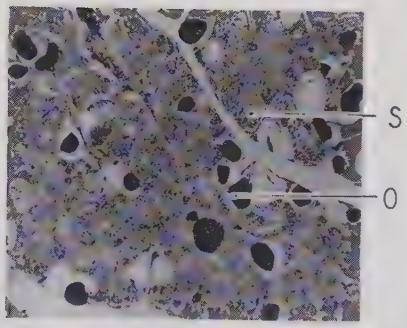

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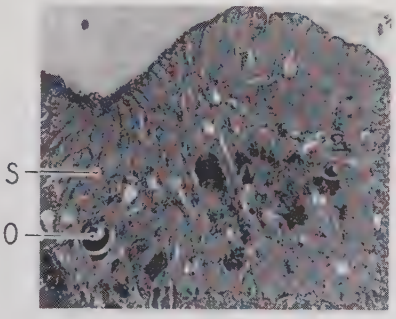

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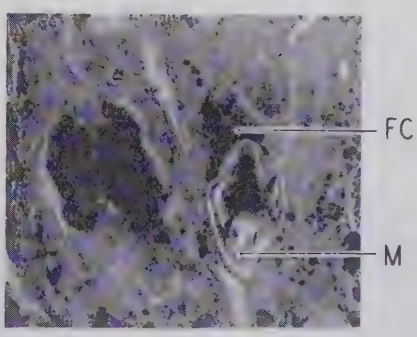

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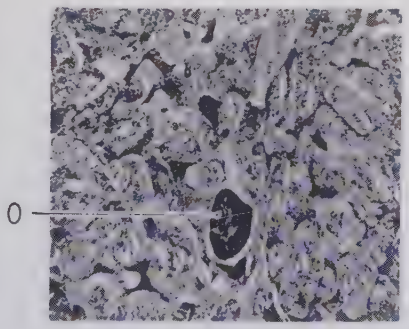

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FISHERIES

Papers of the Michigan Academy of Science, Arts, and Letters
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SIGNIFICANCE OF TRAP-NET SELECTIVITY IN ESTIMATING FISH POPULATION STATISTICS[1]

WILLIAM C. LATTA
Institute for Fisheries Research, Michigan Department of Conservation, Ann Arbor, Michigan

In estimating the size of fish populations in Michigan lakes (G. P. Cooper, 1952; Cooper, 1953; Crowe, 1953; Cooper and Latta, 1954; Cooper and Schafer, 1954), much of the work has been done with trap nets. Although it was realized from the beginning that the trap nets were selective for different species and did not adequately sample the smaller fishes (because of mesh size), we noted only recently that these nets were also selective for size among the larger fishes. The explanation for size selectivity probably lies in the behavior of the species rather than in the physical function of the net.

In recent population studies where marked recoveries were measured, the mean total length of recoveries was usually larger than the mean length of the total marked group (Table I). Further, estimates of mortality rate and size of population in many instances were not reasonable, to judge by other information. We observed these phenomena in studies made at Whitmore Lake, 1955 and 1956; Sugarloaf Lake, 1955; Fine Lake, 1955; and Fife Lake, 1956. Apparently the larger fish are easier to catch than are the smaller fish, and estimates of mortality rate and population size must be adjusted accordingly.

Estimates of population numbers, where trap nets are used, should apparently be made for each size group of a species. In stream populations, where the sample is taken with an electric shocker, which is selective for size also, this has been done (E. L. Cooper, 1952; Sullivan, 1956). Also, for mortality estimates, the trap-net sample of fish which is used to show the decrease in numbers of fish in successive age groups must be adjusted for net selectivity.

[1] This study utilizes data on population statistics which were worked up by G. P. Cooper, R. N. Schafer, and myself and reported at the 1957 meeting of the American Fisheries Society in Las Vegas, Nevada. The problem of investigating the factor of net selectivity was turned over to me. D. W. Hayne reviewed the data and suggested the formula for estimating populations by size classes.

TABLE I

MEAN TOTAL LENGTH IN INCHES AND NUMBER OF FISH, IN MARKED (M) AND RECOVERED (R) CATEGORIES, IN FIVE STUDIES OF POPULATION NUMBERS FOR TEN SPECIES OF FISH

Species	Whitmore, 1955		Whitmore, 1956		Sugarloaf, 1955		Fife, 1955		Fine, 1956	
	M	R	M	R	M	R	M	R	M	R
Bluegill (*Lepomis macrochirus*)										
Mean total length	6.1	6.6	6.2	6.8	5.6	5.7	6.5	7.3	...	...
Number	1,120	71	1,340	48	456	24	795	33	...	...
Rock bass (*Ambloplites rupestris*)										
Mean total length	6.1	6.8	...	...	7.4	7.9	7.5	8.5	...	...
Number	267	22	...	...	463	80	739	801	...	...
Pumpkinseed (*Lepomis gibbosus*)										
Mean total length	5.6	6.6	...	...	...	...	...	...	...	...
Number	763	31	...	...	...	...	...	...	...	...
Black crappie (*Pomoxis nigromaculatus*)										
Mean total length	...	...	...	...	9.1	9.6	8.6	8.9	...	...
Number	...	...	...	...	151	20	382	71	...	...
Warmouth (*Chaenobryttus gulosus*)										
Mean total length	...	...	...	...	6.6	6.9	...	...	...	...
Number	...	...	...	...	117	14	...	...	...	...
Largemouth bass (*Micropterus salmoides*)										
Mean total length	12.9	14.0	12.7	14.1	...	...	14.2	14.3	...	...
Number	477	41	533	23	...	...	617	182	...	...
Smallmouth bass (*Micropterus dolomieui*)										
Mean total length	...	...	...	...	...	...	13.3	13.8	...	...
Number	...	...	...	...	...	...	319	102	...	...
White sucker (*Catostomus commersoni*)										
Mean total length	...	...	...	...	...	...	17.3	18.2	...	...
Number	...	...	...	...	...	...	165	138	...	...
Yellow bullhead (*Ictalurus natalis*)										
Mean total length	9.2	10.4	8.8	10.2	10.1	10.5	...	...	8.9	9.7
Number	171	79	148	28	188	653	...	...	581	62
Brown bullhead (*Ictalurus nebulosus*)										
Mean total length	9.1	9.4	...	...	...	...	...	...	10.5	11.1
Number	309	16	...	...	...	...	...	...	465	27

Gear and Methods

The trap net used in these studies, a commercial type, has a single pot 5 feet by 3 feet by 8 feet, with 2-inch stretched mesh. The heart is 12½ feet long with 2½-inch mesh; and the wings are 10 feet long with 3-inch mesh. The lead is 150 feet long by 3 feet deep with 3-inch mesh. Crowe (1950) described the construction and use of small trap nets of this type.

The netting stations on each of these four lakes were selected by the use of a numbered grid overlying the map of the lake and a table of random numbers. Six trap nets were used, and each was moved daily to another randomly selected station. The netting was continuous for about 30 or 40 days; approximately 200 net sets were made on each lake. A few of the stations were repeated when the system of random numbers called for it. More details of the procedure are provided in Cooper and Latta, 1954, and Cooper and Schafer, 1954.

Fish were marked by clipping a fin and were released at the station of capture. All of the less abundant fishes taken in the nets and a sample of the more abundant fishes, determined by a systematic schedule, were measured and samples of scales taken. Age and length frequency distributions were prepared for all species with sufficient numbers in the sample; an example is Table II.

The differences in catchability with size is demonstrated, using some representative species from Table I, by plotting the weighted R/M percentages (the recaptured marked fish, R, divided by the total number of marked fish, M) against the length, for the various size classes (Figs. 1–5). In order to reduce some of the variability resulting from the small numbers in each size class of the recaptured marked fish, a weighted, moving average of three was used, including both R and M. The R/M percentage was based on these averages (Table III). In these population studies, where about the same number of fish are marked at each lift of the nets, the fraction R/M is approximately proportional to the average capture probability for the marked fish. For those species in which only a sample of the marked fish was measured, the number of marked fish in each size class was estimated on the basis of the frequency distribution of the sample (Table III).

TABLE II

AGE AND LENGTH FREQUENCY DISTRIBUTION OF BLUEGILLS, CAPTURED AT WHITMORE LAKE, 1955, WITH A CALCULATION OF SURVIVAL RATE (s)

Size in Inches	Age Group						Total Number of Fish
	III	IV	V	VI	VII	VIII	
4.2–4.3	3	1	...	..	...	...	4
4.4–4.5	8	6	...	..	...	...	14
4.6–4.7	4	5	...	..	...	...	9
4.8–4.9	10	17	...	..	...	...	27
5.0–5.1	3	42	1	..	...	...	46
5.2–5.3	2	76	6	..	...	...	84
5.4–5.5	1	105	9	..	...	...	115
5.6–5.7	..	87	9	..	...	...	96
5.8–5.9	..	94	18	..	...	...	112
6.0–6.1	..	77	22	..	...	...	99
6.2–6.3	..	62	53	..	...	...	115
6.4–6.5	..	39	59	..	...	...	98
6.6–6.7	..	17	47	..	...	...	64
6.8–6.9	..	13	42	1	...	...	56
7.0–7.1	..	5	44	2	...	..	51
7.2–7.3	..	2	36	5	...	...	43
7.4–7.5	..	1	29	2	...	...	32
7.6–7.7	..	..	12	10	...	...	22
7.8–7.9	..	..	9	9	...	...	18
8.0–8.1	..	..	...	10	...	...	10
8.2–8.3	..	..	1	2	...	...	3
8.4–8.5	..	..	...	..	...	...	...
8.6–8.7	..	..	...	1	...	...	1
8.8–8.9	..	..	...	..	...	1	1
Total	31	649	397	42	...	1	1,120

$$\text{Survival } (s) = \frac{\text{V} + \text{VI} + \text{VII} + \text{VIII}}{\text{IV} + \text{V} + \text{VI} + \text{VII}}$$

$$s = \frac{440}{1088} = 0.40$$

An examination of Figures 1 to 5 shows the trend of increase in the percentage of recaptures of marked fish with increase in size. For the bluegill (Fig. 1) the increase is small up to a length of about 7.0 inches and then rapid for larger fish. This is shown by the bluegills from Whitmore Lake, 1955 and 1956, and Fife Lake, 1956. The

TABLE III

Populations of Bluegills by Sizes

Size in Inches	Total Number Measured	Estimated Number Marked M_i	Total Number Recaptured R_i	R/M as Per Cent†	Adjusted R_i	Population‡ P_i
4.2–4.3	4	14	..*	...	..	.....
4.4–4.5	14	49	..	...	..	.....
4.6–4.7	9	31	1	...	1	4,465
4.8–4.9	27	94	1	0.8	1	4,465
5.0–5.1	46	160	1	0.7	1	12,880
5.2–5.3	84	293	2	0.6	2	21,609
5.4–5.5	115	400	2	0.9	4	20,200
5.6–5.7	96	334	5	1.2	4	14,111
5.8–5.9	112	390	6	1.8	7	11,059
6.0–6.1	99	345	8	1.8	6	10,091
6.2–6.3	115	401	6	1.7	7	11,686
6.4–6.5	98	342	5	1.7	6	9,918
6.6–6.7	64	223	5	2.0	4	6,328
6.8–6.9	56	195	5	2.0	4	4,851
7.0–7.1	51	178	2	2.5	4	4,049
7.2–7.3	43	150	6	2.5	4	2,887
7.4–7.5	32	112	3	4.1	5	1,310
7.6–7.7	22	77	5	4.8	4	779
7.8–7.9	18	63	4	6.5	4	527
8.0–8.1	10	35	3	7.0	3	361
8.2–8.3	3	10	..*	...	..	...
8.4–8.5	..	..	..	...	..	...
8.6–8.7	1	3	1	...	1	21
8.8–8.9	1	3	..*	...	..	...
Total	1,120	2,137	71	...	72	141,597

* Size classes without recaptures were combined with the adjacent size class containing recapture(s).

† A weighted moving average of three of R_i and M_i was used to determine the percentage.

‡ Based on an adjusted number of recoveries for each size class, Whitmore Lake, 1955.

sample from Sugarloaf Lake, 1955, contained few fish larger than 6.8 inches and thus lacks the ascending part of the curve for larger fish.

The rock bass data (Fig. 2) from Fife Lake, 1956, show a uniform upward trend. For Whitmore Lake, 1955, and Sugarloaf, 1955,

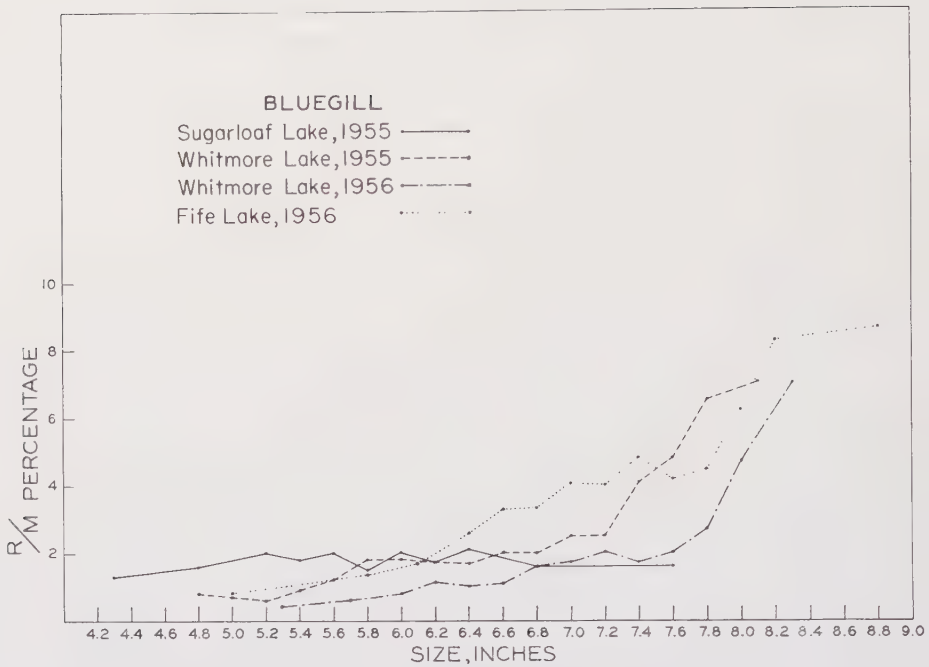

FIG. 1. The percentage of recapture of marked fish plotted against length, in inches, for each size class of bluegills, in three lakes.

the trend is also upward, with size, but more erratic; there were only a few fish in the larger size classes, which may explain some of the variation.

The largemouth bass data (Fig. 3) show more variation than is shown for other species. In 1955 in Whitmore Lake, there was apparently a slight tendency for the larger bass to be caught more readily than the smaller, but in 1956 there was no indication of this. In Fife Lake, 1956, there was an increase in catchability with size up to about 15.0 inches and then a pronounced decrease. Although there is no trend in the data for bass, there is enough variation in catch with size to suggest that size classes should be considered separately in estimates of population size.

Figures 4 and 5 indicate the same tendency for increase in catch with size for the yellow bullhead and brown bullhead in Fine Lake in 1955 and the white sucker in Fife Lake in 1956.

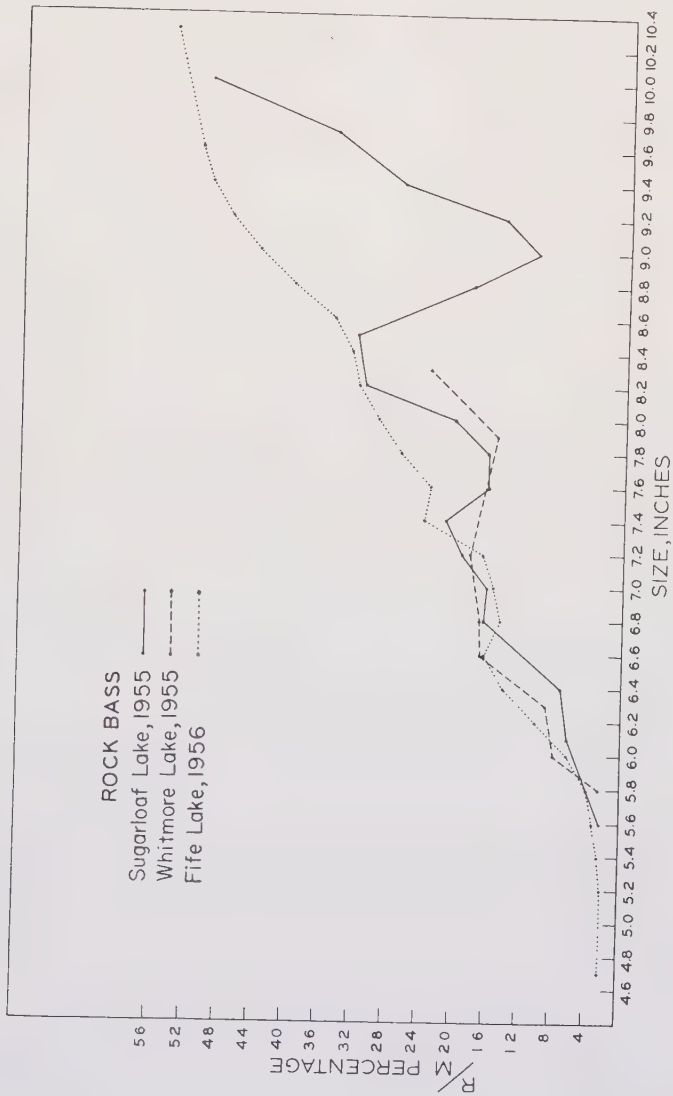

Fig. 2. The percentage of recapture of marked fish plotted against length, in inches, for each size class of rock bass, in three lakes.

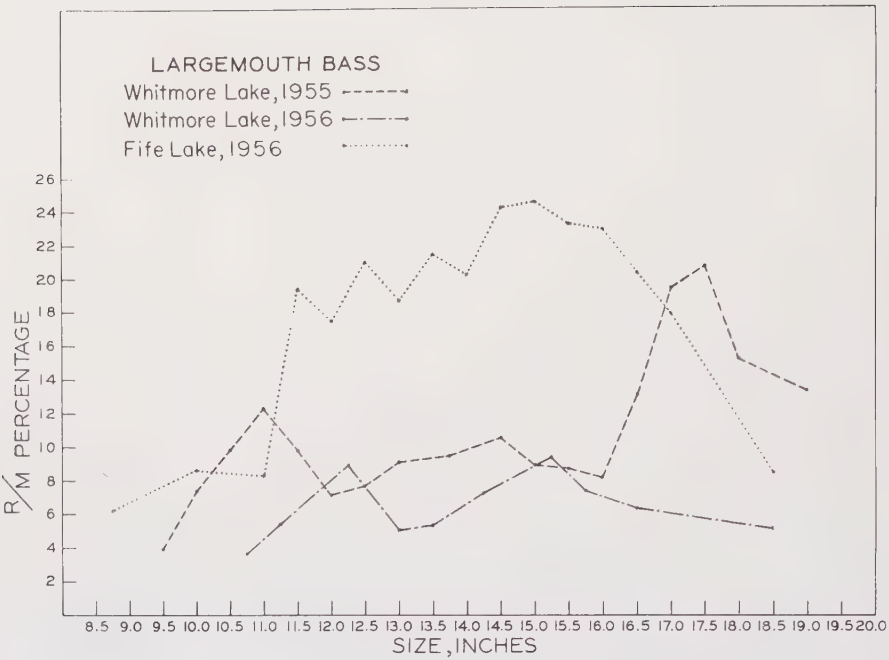

Fig. 3. The percentage of recapture of marked fish plotted against length, in inches, for each size class of largemouth bass, in two lakes.

Causes of Selectivity

My co-workers and I have observed in the field use of these trap nets that they are selective for size and species. The nets seldom catch sunfish below 4.0 inches in length or bass below 7.0 inches. They obviously do not sample yellow perch satisfactorily or, according to Crowe (1950), trout, whitefish, and herring. In Sugarloaf Lake, in the years 1948 through 1955, where anglers harvested 6,000 to 20,000 yellow perch annually, there were only two years in seven in which enough perch were caught in the trap nets to attempt an estimate of the number of yellow perch in the lake.

The selectivity for species probably can be attributed to some unknown behavior characteristic of the fishes involved. The inability of trap nets to capture fish below a certain size has been attributed to the physical dimensions of the mesh. A hypothesis is needed, however, for the selective pattern demonstrated, in the

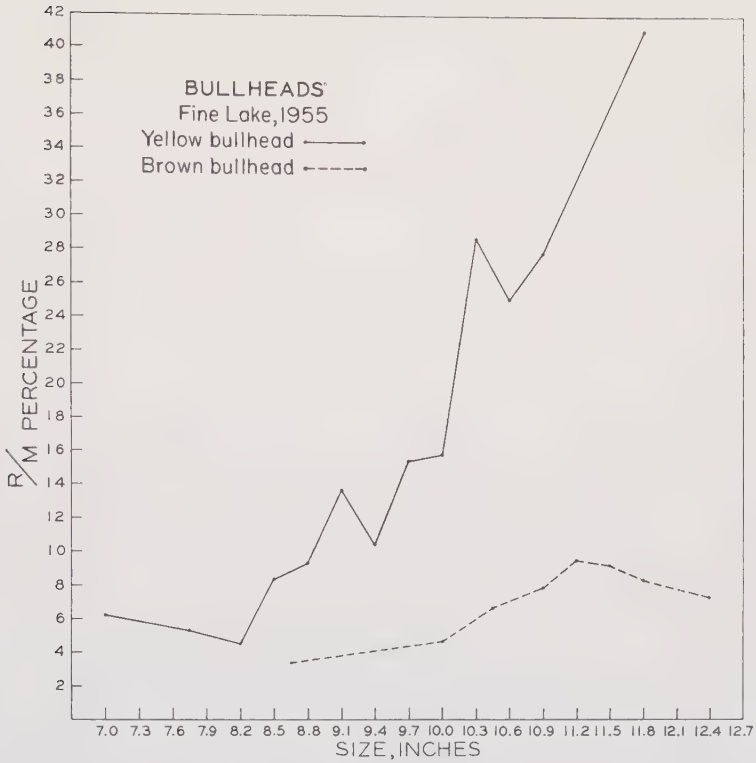

FIG. 4. The percentage of recapture of marked fish plotted against length, in inches, for each size class of yellow and brown bullhead, in Fine Lake.

size classes retained by the netting, where the larger fish appear to be more susceptible to capture than the smaller fish.

A possible explanation might be that the apparent increase in the R/M percentage with increase in size of fish is an artifact of growth. It seems from examining hypothetical data that certain combinations of population structure and rates of growth could produce the appearance of an increasing R/M percentage, just as other combinations could have the opposite effect. However, this explanation is rejected because an examination of the scales indicated the fish were growing very little at the time of each study.

The population estimates at Sugarloaf Lake and Fine Lake were made October 6 to November 10, 1955, and October 11 to November

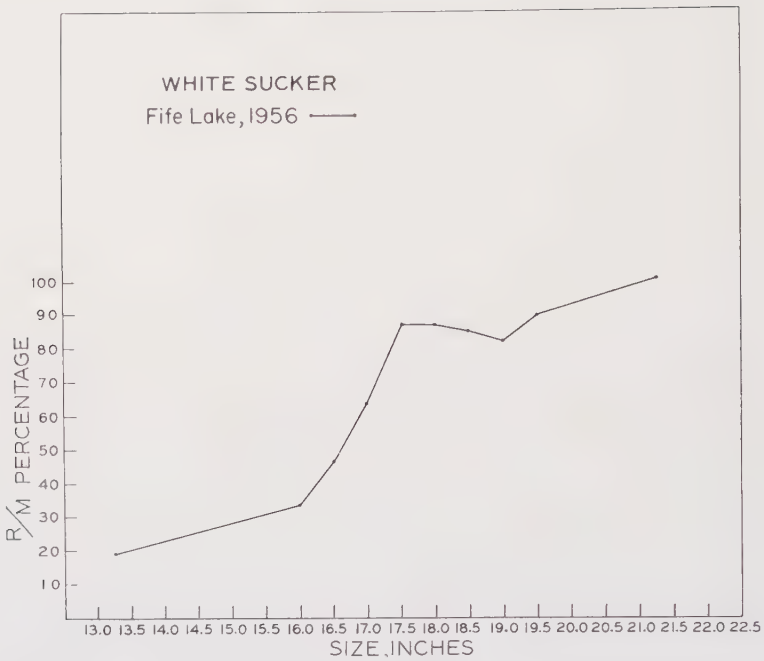

Fig. 5. The percentage of recapture of marked fish plotted against length, in inches, for each size class of white sucker, in Fife Lake.

15, 1955, respectively. Growth of centrarchids and probably other fishes at this time of year, in this region, is practically nil (Spoor, 1938; Hile, 1941; Beckman, 1943). The other population estimates were made during the spring months—Whitmore Lake, April 19 to May 31, 1955, and April 11 to May 23, 1956; Fife Lake, May 3 to June 11, 1956. In all three studies the annulus was being formed, indicating that growth was just beginning. In Fife Lake, where the curves indicating selectivity are the strongest, the percentage of the bluegills with an annulus present on the scales was only 3 per cent; rock bass, 2 per cent; largemouth bass, 3 per cent; and white sucker, 56 per cent. At Whitmore Lake, in 1956, the percentages were bluegill, 6 per cent, and largemouth bass, 19 per cent; in 1955, spring arrived early and the percentages were considerably higher—bluegill, 69 per cent; rock bass, 59 per cent; and largemouth bass, 10 per cent. With growth just beginning in all populations, there is little likelihood that it influenced the curves of selectivity to an important extent.

Some behavior pattern of the fishes seems to be the best explanation of these curves of selectivity. Above the smaller size of fish, there is no physical aspect of the net which should restrain the larger fish of a certain size class. Perhaps the larger fish more actively seek cover than the smaller fish. The larger fish in a net may set up a "peck order" or dominating role which forces the smaller fish to leave (Gerking, 1957). Hansen (1944) showed that both the largemouth bass and bluegill are adept at escaping from hoop nets which are basically similar in design to trap nets. There is no reason to believe that centrarchids and bullheads, which seek or are usually associated with cover, could not easily leave a trap net.

The best explanation is that probably the larger fish, moving more than the smaller ones in satisfying their food or other requirements, are exposed more to capture. Watt (1956) suggested that the greater amount of movement of the larger fish makes them more prone to capture and illustrated the point with data from the recapture of smallmouth bass in South Bay, Manitoulin Island. Likewise, Latta (1957) showed, for tagged smallmouth bass at Waugoshance Point, Lake Michigan, that with an increase in size there was an increase in distance traveled and, correspondingly, an increase in the number of times a fish was captured in a trap net. Eschmeyer, Daly, and Erkkila (1953) and Mraz (1952) found that in Great Lakes water lake trout and yellow perch moved farther with an increase in size. Funk (1957) noted, for rock bass, smallmouth bass, and channel catfish in Missouri streams, that the smaller and the larger fish moved much less than did fish of intermediate sizes. He hypothesized that, as a fish increases in size, competition for a territory to satisfy its needs increases and movement is greater, until the larger fish is able to defend a particular niche.

Effect of Selectivity on Estimates of Population Statistics

The variability in percentage recovery of marked fish with size means that estimates of population numbers should be on the basis of size classes. With the curves of selectivity showing a tendency for a greater recovery of the larger fish, estimates of population size not based on size classes are too small. Likewise, estimates of survival based on a decrease in the number of fish in succeeding age groups are too large. Examples of the change in estimate of population size were calculated from the Whitmore Lake bluegill and largemouth bass data of 1955 and 1956 (Table IV). Here, I

TABLE IV

RESULTS OF ESTIMATES OF POPULATION SIZE BY TWO METHODS FOR BLUEGILL AND LARGEMOUTH BASS IN WHITMORE LAKE, 1955 AND 1956

Year and Method	Bluegill		Largemouth Bass	
	Sublegal (<6.0 in.)	Legal* (⩾6.0 in.)	Sublegal (<10.0 in.)	Legal (⩾10.0 in.)
1955				
Schumacher-Eschmeyer	88,872	47,167	1,278	1,918
Present	88,789	52,808	2,806	2,169
1956				
Schumacher-Eschmeyer	321,110	80,766	.....†	3,440
Present	272,618	109,552	.....	5,160

* The terms legal and sublegal are arbitrary, for there is no minimum size limit on pan fish in Michigan at the present time.

† No recoveries of sublegal marked fish.

have provided a comparison of the population size estimated by the Schumacher-Eschmeyer method for a population as a whole (Schumacher and Eschmeyer, 1943) with the present method for the estimation of population size for each size class.

In the study it was not possible to recompute population estimates by separate size classes by the Schumacher-Eschmeyer method, because for the more numerous fish only a sample of those captured were measured from day to day. But it was possible to approximate the population number for the various size classes, using the estimate of capture probability mentioned earlier. By the present method, developed by Don W. Hayne, the population was estimated for a single size class as:

$$P_i = \frac{M_i^2}{2R_i} + \frac{M_i}{2}$$

where:

M_i = the number of marked fish in i size class;
R_i = the number of recoveries of marked fish in i size class.

The summation of the number of fish estimated for each size equals the total population.

TABLE V

SURVIVAL RATES (s) FOR THE BLUEGILL AND LARGEMOUTH BASS BEFORE AND AFTER CORRECTION FOR NET SELECTIVITY, IN WHITMORE LAKE, 1955 AND 1956

Year	Bluegill	Largemouth Bass
	s^*	s^*
1955		
Before correction	0.40	0.57
After correction	0.28	0.37
1956		
Before correction	0.58	0.69
After correction	0.36	0.54

* Calculated for age-groups IV and above.

Table IV shows the expected larger size of the estimates of the total population when they are made by size classes. The only exception is the sublegal[2] bluegills (less than 6.0 inches in length). There were few recaptures in this category, particularly in the 1956 data, and little upward trend in the R/M percentages with increased length (Fig. 1), which indicates there should be little or no difference in the estimates in a comparison of the two methods at the sublegal size.

Survival (s) is usually calculated from the age distribution of a sample of the population. The survival rate (s), calculated on the basis of a decrease in numbers of succeeding age groups (Ricker, 1945), becomes smaller when it is adjusted for the greater catchability of the larger fish (Table V). Table II illustrates the method, before an adjustment is made, using the bluegill data for 1955 from Whitmore Lake.

This survival rate was corrected by distributing the population estimates for each size class (P_i) over the age distribution of the sample; e.g., in the 6.6- to 6.7-inch size class of bluegills from Whitmore Lake, 1955, the P_i of 6,328 was proportioned to age-groups IV and V, according to the respective numbers 17 and 47 in the original sample (Tables II and VI). Then, using the total age distributions, a corrected survival rate (s) was calculated (Table VI). Here, in the 1955 Whitmore Lake data for the bluegill, is a change in s from 0.40 before correction to 0.28 after correction (Table V). Like-

[2] The terms sublegal and legal are arbitrary, for there is no minimum size limit on pan fish in Michigan at the present time.

TABLE VI

AGE AND LENGTH FREQUENCY DISTRIBUTION OF BLUEGILLS, USING ESTIMATED NUMBERS IN EACH SIZE CLASS (P_i), WHITMORE LAKE, 1955, WITH A CALCULATION OF AN ADJUSTED SURVIVAL RATE (s)

Size in Inches	Age Group						Population P_i
	III	IV	V	VI	VII	VIII	
4.2–4.7	2,481	1,984	...	...	...	...	4,465
4.8–4.9	1,654	2,811	...	...	...	...	4,465
5.0–5.1	840	11,760	280	...	...	...	12,880
5.2–5.3	514	19,551	1,544	...	...	...	21,609
5.4–5.5	176	18,443	1,581	...	...	...	20,200
5.6–5.7	...	12,788	1,323	...	...	...	14,111
5.8–5.9	...	9,282	1,777	...	...	...	11,059
6.0–6.1	...	7,849	2,242	...	...	...	10,091
6.2–6.3	...	6,300	5,386	...	...	...	11,686
6.4–6.5	...	3,947	5,971	...	...	...	9,918
6.6–6.7	...	1,681	4,647	...	...	...	6,328
6.8–6.9	...	1,126	3,638	87	...	...	4,851
7.0–7.1	...	397	3,493	159	...	...	4,049
7.2–7.3	...	137	2,475	344	...	...	2,887
7.4–7.5	...	41	1,187	82	...	...	1,310
7.6–7.7	...	...	425	354	...	...	779
7.8–7.9	...	...	264	264	...	...	527
8.0–8.3	...	...	28	333	...	...	361
8.6–8.9	...	...	...	10	...	10	21
Total	5,665	98,097	36,261	1,633	...	10	141,597

$$\text{Survival } (s) = \frac{\text{V} + \text{VI} + \text{VII} + \text{VIII}}{\text{IV} + \text{V} + \text{VI} + \text{VII}}$$

$$s = \frac{37{,}904}{135{,}991} = 0.28$$

wise, there is a decrease in s for the bluegill in 1956 and the largemouth bass in 1955 and 1956. These survival rates are not to be considered definitive because the method of calculation assumes equal recruitment of each year class. These data do not fulfill this requirement. Also there is evidence that smaller fish of the youngest age group (age-group IV) used were not sampled completely, even though the frequency distribution of age-group IV appears normal (Table II). The survival rates are presented only as an example of the

change in rate that takes place with a correction for the greater catchability of the larger fish.

Conclusions

There is no doubt that the described trap nets are selective for the larger fish of a size class above the minimum size imposed by the physical dimensions of the net. In all probability this selectivity can be attributed to the behavior of the fish. The procedure developed in Michigan of randomly selecting numerous netting stations in a lake and moving the nets daily (Cooper and Latta, 1954) has ensured, probably better than any other approach, that the sample will reflect the true proportion of marked to unmarked fish in the lake. Then an estimate based on size classes corrects for the variation in reaction of the fish to the nets that may be associated with size.

It is essential in the estimating of population statistics that consideration be given to the selectivity of the fishing gear and that this be corrected for the variation in the final analysis. To quote D. B. DeLury (1954), commenting on estimates of animal populations, "All of our theory is developed, implicitly or explicitly, on the assumption that sampling is random." At the present time the attainment of a random sample of a natural population appears as almost impossible, but the goal must be kept in mind, and such things as the consideration of the behavior of fish to the fishing gear not neglected.

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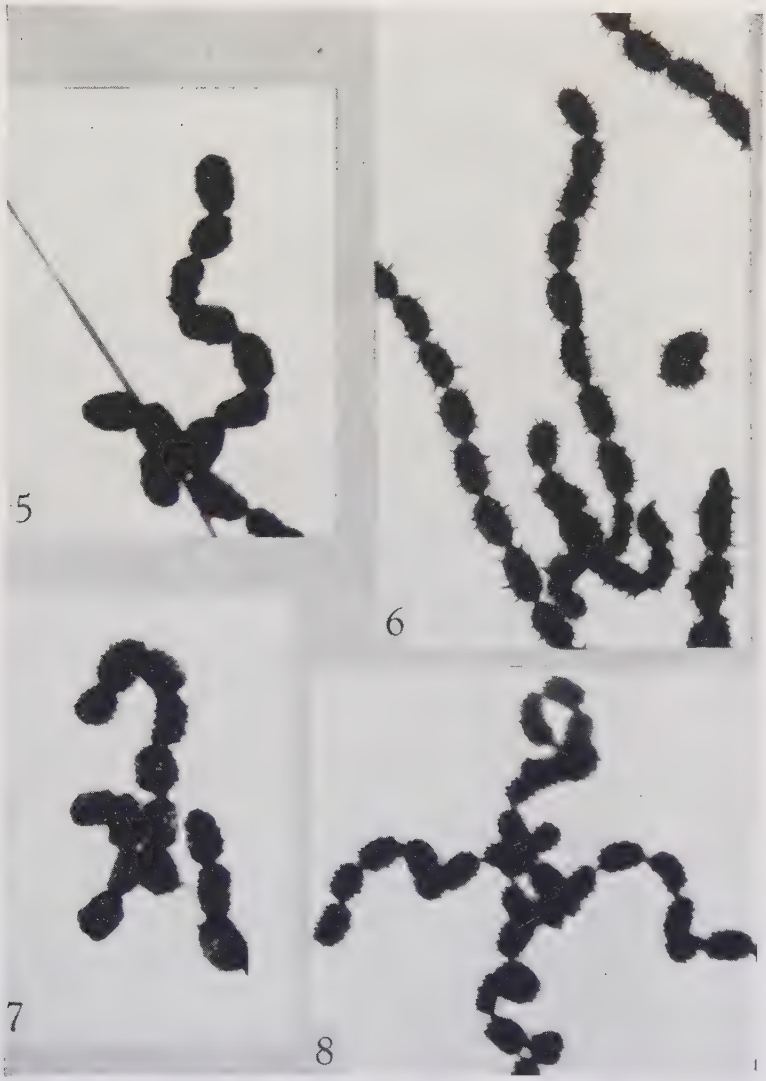
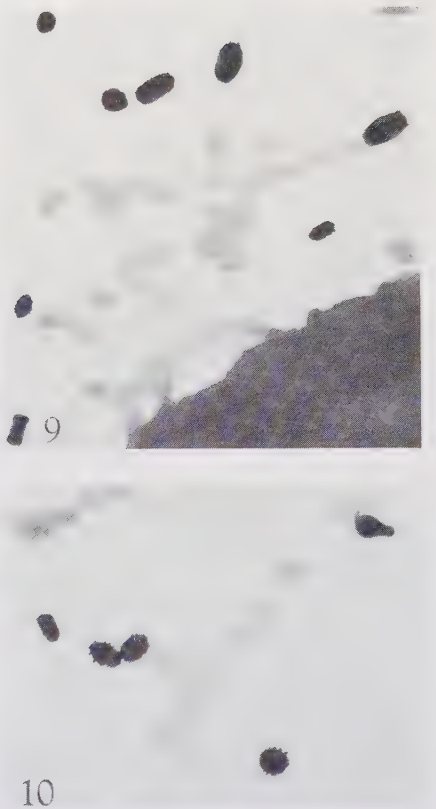
BOTANY

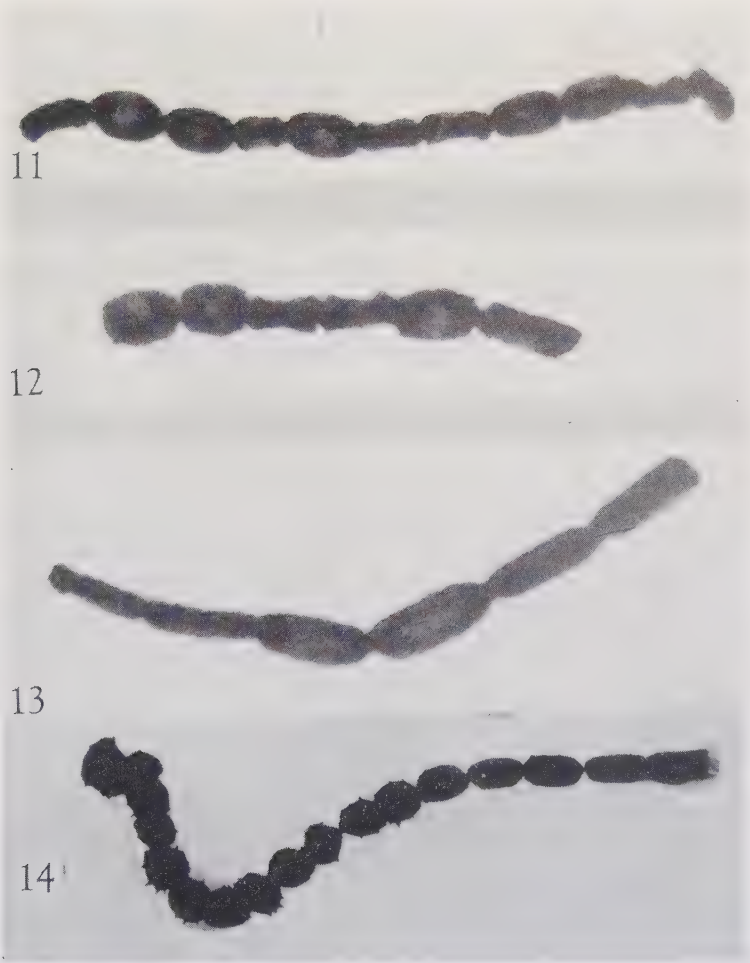
FIGS. 1–4. A smooth-spored isolate (F 10) on starch (Fig. 1), Bennett's agar (Fig. 2), Czapek's agar (Fig. 3), and Krainsky's agar (Fig. 4).



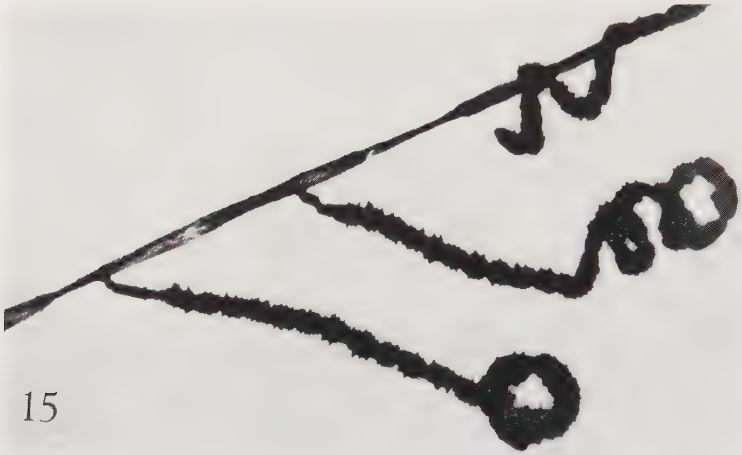
FIGS. 5–8. A spiny-spored isolate (A 1) on Czapek's agar (Fig. 5), potato (Fig. 6), Bennett's agar (Fig. 7), and potato glucose (Fig. 8).



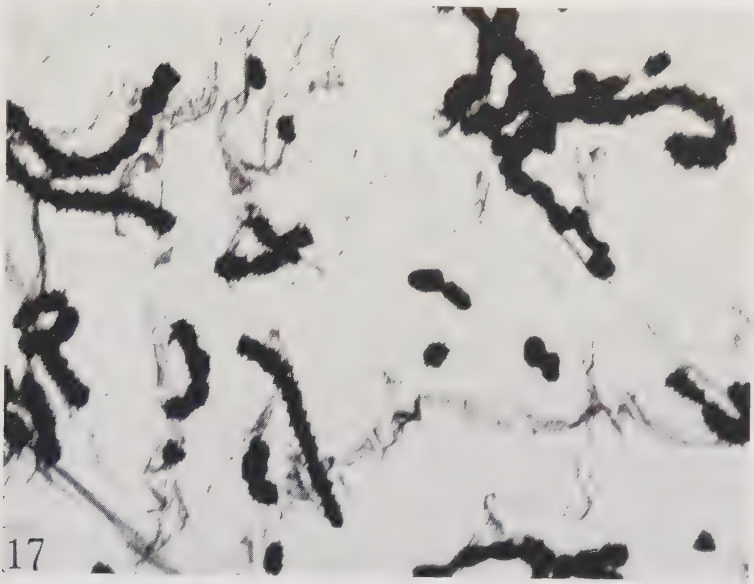
FIGS. 9–10. Spore variation within a field: (A 1) Krainsky's (Fig. 9) and (A 5) Bennett's (Fig. 10).

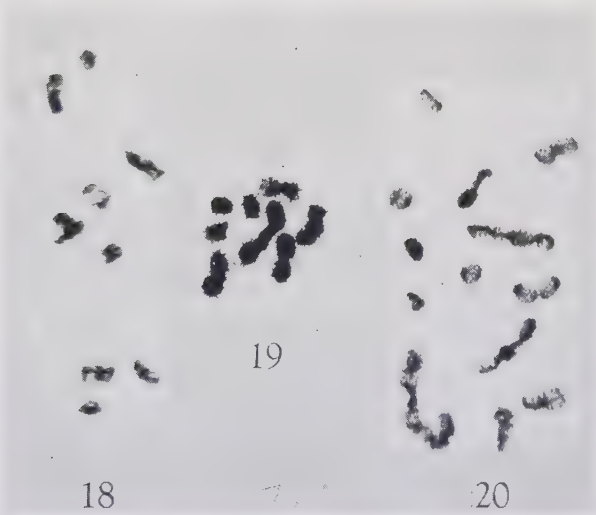


FIGS. 11–14. Variation of spores within a chain: (A 5) on starch (Fig. 11), (A 5) Bennett's (Fig. 12), (F 55) Bennett's (Fig. 13), (H 49) nitrogen-free agar (Fig. 14).



FIGS. 15–17. Spiny walls of aerial hyphae: (B 36) Bennett's (Fig. 15) and (A 43) after 9½ weeks on Czapek's agar (Fig. 16), (B 61), (Fig. 17).





FIGS. 18–20. Spores after 15 months on agar media: (C 53) Bennett's agar (Fig. 18), (A 90) Bennett's agar (Fig. 19), (A 90) Bennett's agar (Fig. 20).

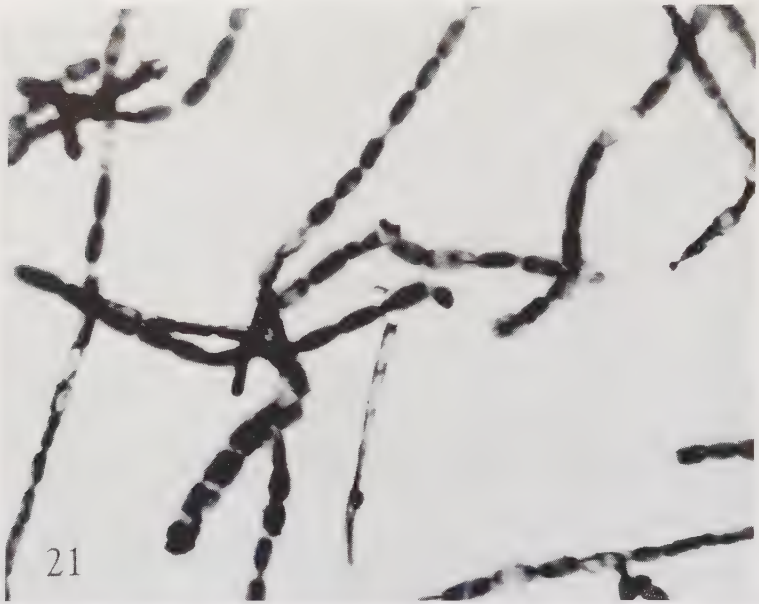


FIG. 21. Smooth-walled spores showing hyphal constrictions (A 31) Bennett's after 4 weeks.

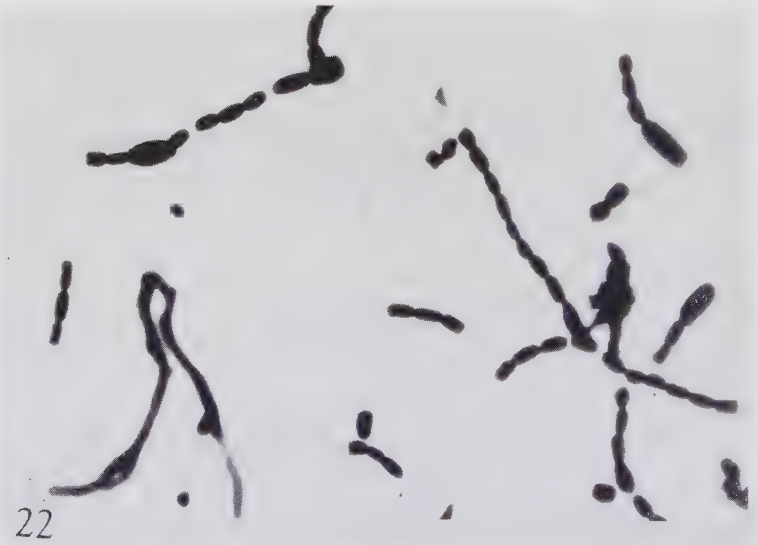
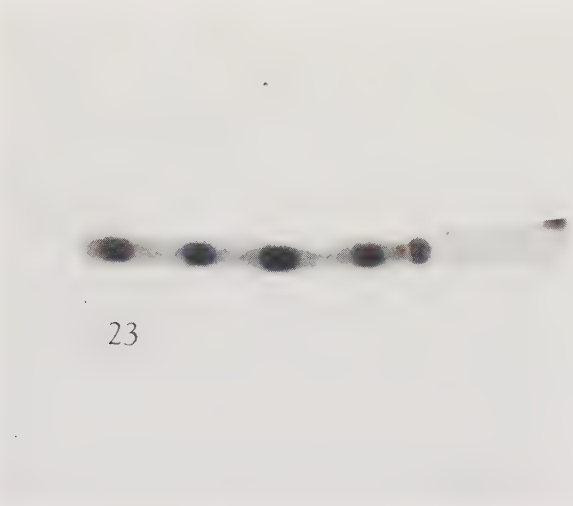


FIG. 22. Smooth-walled spores showing diversity of sizes within a field (155–57).



FIGS. 23–24. Metachromatic granules: (E 67) nitrogen-free agar (Fig. 23), (A 35) Krainsky's 5 weeks (Fig. 24).

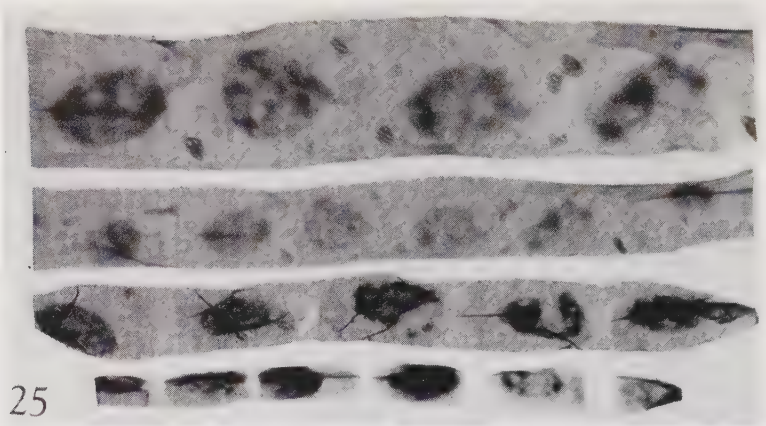


FIG. 25. Nuclei in aerial filaments (B 43) starch agar 4 weeks. In all instances the filaments and spores are somewhat less than 1 μ in diameter. No attempt has been made at uniformity of magnification in the illustrations.

The spines are protuberances of the wall of the hypha within which the spores form, as Kutzner (1956) has shown. Considerable lengths of spiny hyphae were observed prior to the delimitation of spores (Fig. 15); at the base of intact spore chains; as old and partly shrunken, asporous hyphae (Fig. 16); and as detached segments of mature hyphae which could be construed as long spores (Fig. 17).

Spiny spores, then, possess an outer wall of hyphal origin. Our observations do not give information on any additional inner wall or walls. The interior of the spore is uniformly opaque except in old spores where the contents have apparently disappeared (Fig. 20).

Smooth spores are either encased by smooth-walled hyphae (Fig. 21) or the hyphae disintegrate to release spores with unornamented coats or membranes. The spores of Nocardia observed by Gordon and Mihm (1958) closely resemble the smooth spores of Streptomyces.

On a given culture medium an organism presents a complex assemblage of spores of varying sizes, shapes, surfaces, and densities (Figs. 9–10). Whether this assemblage is sufficiently constant and intelligible to an experienced observer to be used in identifying isolates remains to be seen. The diversity of spores within a field and within a chain (Figs. 10–15) is considerable. Erikson (1948) has shown that sister spores of the same chain gave dissimilar growths which remained so throughout ten successive transplants.

Nuclei

Attempts to demonstrate nuclei in substratal mycelium met with no success. Electron opaque granules were rather commonly found (Fig. 23). These had the "right" size and shape and spacing for nuclei. The light microscope indicated, however, that they were metabolic products easily detected as metachromatic with methylene blue. Granules may persist in old and even collapsed filaments (Fig. 24).

We believe that nuclei have been observed in aerial hyphae in isolate B43 (Fig. 25). They appear throughout all of the filaments just prior to sporulation. Further nuclear studies are being made to gain more information on the life cycle of Streptomyces.

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ADDITIONS TO THE PHYCOMYCETE FLORA OF THE DOUGLAS LAKE REGION. IV. NEW RECORDS AND NOTES FOR 1956–1957*

FREDERICK K. SPARROW AND WILLIAM J. KOCH
University of Michigan and University of North Carolina

The following is an account of the Phycomycetes collected during the summers of 1956 and 1957 in the vicinity of the University of Michigan Biological Station at Douglas Lake, Cheboygan County, Michigan. Many of these are either new to the region, new to the United States, or have some other features worthy of note. Previous accounts of the Phycomycetes from this region have been published by Johnson (1950), Sparrow (1952), Sparrow and Barr (1955), Paterson (1956), and Johns (1956).

Fungi Collected

Chytridiales

Micromyces intermedia (Canter) Sparrow.—Parasitic in *Zygnema sp.*, in association with *M. zygogonii*, Smith's Bog, Cheboygan County, June 26, 1957.

This species has not hitherto been reported from the United States. It fits in most details Canter's account of her species, including the radial splitting of the soral wall (Pl. I, Figs. *E–F*). We saw no spiny prosori as did she, a fact due, perhaps, to the scantiness of our material.

A chytrid, probably a species of *Phlyctidium*, was found parasitic on the sorus of this species (Pl. I, Fig. *G*). It has a narrowly obpyriform sporangium, 27 × 3–7 μ, with a tenuous, short, apparently unbranched needlelike rhizoid that penetrates the host. Since no zoospore discharge was witnessed the generic disposition of the fungus remains in doubt.

Micromyces mirabilis (Canter) Sparrow.—Parasitic in *Closterium sp.*, Bryant's Bog, Cheboygan County, July 14, 1957.

The large, 55–60 μ × 42–50 μ, dark spiny prosori of this species approach those of *M. ovalis* var. *giganteus* Sparrow and Barr in size.

* Contribution from the Biological Station, University of Michigan.

Although germinated prosori were not found, the ungerminated ones were strikingly like those of Canter's species, and we have no doubt as to their identity. Like the previous chytrid, this one has not been heretofore reported from the United States.

Olpidium utriculiforme Scherffel.—Parasitic in *Cosmarium sp.*, Nichol's Bog, Cheboygan County, July 16, 1956.

A species hitherto unreported from the United States.

The fungus reported by Canter from England on *Closterium* and assigned to this species strongly resembles, as she suggests, *Mitochytridium ramosum.*

Rhizophydium couchii Sparrow.—On *Spirogyra sp.*, mouth of Bessey Creek, Douglas Lake, Cheboygan County, July 1, 1956. A new record for the region.

Rhizophydium sp.—On *Liquidambar* pollen bait; debris from Mud Lake, Cheboygan County, July 7, 1956.

Inasmuch as no rhizoidal system could be detected within the substratum, the generic disposition of this striking species is a matter of doubt.

Immature sporangia (Pl. I, Fig. *A*) were somewhat dome-shaped and rested on a very broad base on the surface of the pollen grain. No perceptible papilla was observed. Upon maturity of the zoospores they emerged by a sudden bulging of the whole inert mass (Pl. I, Fig. *B*). As discharge continued the sporangial orifice broadened. Finally, individuals of the motionless mass of spores at the broad mouth of the sporangium initiated flagellar movements and swarmed away. They were somewhat ovate, 2 μ in diameter, and bore an eccentric globule. The empty sporangia (Pl. I, Figs. *C–D*) were elegant objects, broad and beakerlike, with strongly reflexed rim. They were 12–25 μ high by 22–30 μ broad and were consistently broader than high. The orifice was 15–22 μ in width and always nearly as broad as the greatest sporangial diameter. The smooth rim of the sporangium would almost seem to necessitate an operculate type of dehiscence as in *Chytridium lateoperculatum* Scherffel parasitic on a zoocyst of *Vampyrella*, but no operculum was ever observed.

The chytrid probably is a new species, but until details of the endobiotic system are known, its generic disposition is uncertain. It is truly remarkable that this microscopic fungus sporangium should so strikingly resemble the beakers made by prehistoric man.

The sporangia bear a striking resemblance to the smooth-walled ones of *Rhizophlyctis harderi* Uebelmesser. No rhizoidal outgrowths, however, were ever seen, a feature said to distinguish the last-named species.

Phlyctochytrium sp.—On *Liquidambar* pollen bait, Mud Lake bog, July 25, 1957.

This curious chytrid (Pl. I, *H–K*) was isolated in very limited numbers from *Sphagnum* debris. Unfortunately, its zoospore discharge was not seen. The body of the sporangium was highly irregular in shape, 12–15 μ high by 15–20 μ broad and bore two, rarely more, simple or bifurcated solid spines. There was definite evidence that a portion of the original zoospore cyst remained unexpanded as in *Chytridium schenkii* and allied forms.

The endobiotic part was subspherical or irregularly saccate. There was some but not convincing evidence for the presence of rhizoids. It is hoped further studies will supply the missing data on this interesting fungus.

Phlyctochytrium unispinum Paterson.—On filaments of *Zygnema sp.*, Smith's Bog, June 26, 1957.

This is the second record of the occurrence of this species.

Phlyctochytrium aureliae Ajello.—On *Liquidambar* pollen bait, Bryant's Bog, June 22, 1956; Nichol's Bog, July 16, 1956; insect exuviae, Hardbottom Bog (Emmett County), July 1, 1946; snake skin bait, Bryant's Bog, July 25, 1956 (coll. R. O. Stein).

This species has previously been reported only on decaying vegetation, insect exuviae, and shrimp chitin bait. Its utilization of pollen as a substratum is of considerable interest from a physiological standpoint.

Phlyctochytrium mucronatum Canter.—Parasitic on *Closterium sp.*, Bryant's Bog, June 20, 1956.

This species has been heretofore recorded only from England.

Phlyctochytrium chaetiferum Karling.—On *Liquidambar* pollen bait; debris from Bessey Creek, Douglas Lake, July 7, 1956.

This species has hitherto been known only as a saprophyte of algae.

Phlyctochytrium punctatum Koch.—*Liquidambar* pollen bait, Nichol's Bog and Hardbottom Bog, July 19, 1956.

A new species to the region and the second record of its occurrence.

Phlyctochytrium quadricorne (de Bary) Schroeter.—*Liquidambar* pollen bait; Smith's Bog, July 2, 1956.

A species heretofore reported as living only on algae.

Phlyctochytrium irregulare Koch.—*Liquidambar* pollen bait; Smith's Bog, July 2, 1956; soil by Community Church, Topinabee, Cheboygan County, July 16, 1956.

The first record of this fungus in the region and the second of its occurrence.

Phlyctochytrium sp.—All collections from soil. *Liquidambar* and *Pinus spp.* pollen bait; Smith's Bog, July 2, 1956; roadside, Topinabee, base of fire tower, Biological Station, head of trail to Gorge, Biological Station, July 16, 1956; by Shell Gasoline Station, Cross Village (Emmett County), beech-maple forest 1 mile north of Cross Village, sand dune 2 miles north of Cross Village, pine forest, Wilderness Park, July 20, 1956; mouth of Montreal River, Ontario (coll. R. O. Stein), August 1, 1956; Taquahmanon Falls Park, Chippewa County (coll. Harry Thiers), July 10, 1954.

This is the unnamed species from Germany described and figured by Reinboldt (1951). In spite of its apparent ubiquity it has not heretofore been reported from the United States.

Blyttiomyces helicus Sparrow and Barr.—Pine pollen bait; Bryant's Bog, June 26, 1956; Hardbottom Bog, July 1, 1956; Nichol's Bog, July 10, 1957.

This striking species, hitherto known only from Michigan, has recently been reported from Germany by Rieth (1956). He found, as did Sparrow and Barr, endobiotic, smooth-walled resting spores and suggests that these probably belong to the fungus. Until they germinate, however, this cannot be demonstrated with certainty.

The easiest strain on pollen to propagate yet found is that recovered from Hardbottom Bog.

The more ubiquitous *Blyttiomyces spinulosis* was again found in

the region on zygospores of *Spirogyra*, namely, at Smith's Bog on June 26, 1957.

Entophlyctis confervae-glomeratae (Cienk.) Sparrow.--Parasitic on *Eremosphaera viridis*, Bryant's Bog, August 12, 1956.

Eremosphaera has not heretofore been reported as a host for this fungus.

Polychytrium aggregatum Ajello.—On shrimp chitin bait; debris, Bryant's Bog, from under ice, April 8, 1954 (coll. Sparrow, Johns, Paterson), July 10, 1957; insect exuviae, Hardbottom Bog, July 1, 1956.

This interesting and imposing chytrid is readily recoverable on chitin bait from the Bryant's Bog site.

Obelidium mucronatum Nowak.—On shrimp chitin bait; debris from mouth of Bessey Creek, Douglas Lake, July 26, 1956.

The first report of this very rare chytrid from the region and the third from the United States.

Chytridium olla Braun.—On vegetative (suffultory) cells and oögonia of *Oedogonium sp.*; Smith's Bog, June 26, 1956 (coll. R. M. Johns).

Only rarely is this species found on any but oögonial cells of the host. Its presence on a suffultory cell is therefore of interest.

Chytridium oedogonii Couch.—Basal cell of *Oedogonium sp.*, Lancaster Lake, June 28, 1957.

Not reported before from the state.

Chytriomyces hyalinus Karling.—On shrimp chitin bait; debris from mouth of Bessey Creek, Douglas Lake, July 26, 1956; Bryant's Bog, July 27, 1956.

This is the first report of this species in the United States. It commonly occurs in company with *Polychytrium aggregatum* and *Phlyctochytrium aureliae* on chitin bait.

Chytriomyces appendiculatus Karling.—On shrimp chitin bait; Smith's Bog, July 26, 1956.

This is the first report of the species since its original discovery ten years ago.

Hyphochytriales

Rhizidiomyces hirsutus Karling.—On *Liquidambar* pollen bait; dried soil from shore of mouth of Bessey Creek, Douglas Lake, July 8, 1956.

The first report of the fungus since its discovery in Brazil. This same species was recovered on cucurbit pollen bait from soil around Ann Arbor by H. Teter in 1942.

Hyphochytrium catenoides Karling.—In *Liquidambar* pollen bait; soil, mouth Montreal River, Ontario, August 18, 1956 (coll. R. O. Stein); soil, Hardbottom Bog, recovered November 7, 1956.

This rare fungus was not known to utilize pollen. It has not hitherto been reported from the Douglas Lake area.

Olpidiopsis schenkiana Zopf.—On *Spirogyra sp.*, north shoreline of Burt Lake, June 24, 1956.

Only the sporangial stage was seen. The fungus has not hitherto been reported from the area of the Biological Station.

This is the third record of its occurrence in the United States.

Lagenidium pygmaeum Zopf.—In *Liquidambar* pollen bait; soil from head of trail to Gorge by Biological Station, soil by firetower, Biological Station, July 16, 1956; soil, Hardbottom Bog, Emmett County, recovered February 18, 1957.

Only zoosporangial thalli were found.

Lagenidium oedogonii Scherffel.—On vegetative cells of a macrandrous species of *Oedogonium*. Nichol's Bog, July 10, 1957.

The species has not been reported from our area. This is the third collection of it in the United States.

Entomophthorales

Ancylistes closterii Pfitzer.—In *Closterium sp.*, Bryant's Bog, July 10, 1957.

Ancylistes netrii Couch.—In *Netrium sp.*, Nichol's Bog, July 10, 1957.

This is the first record of the occurrence of this species since its discovery nearly a decade ago. It is very common at the site mentioned above.

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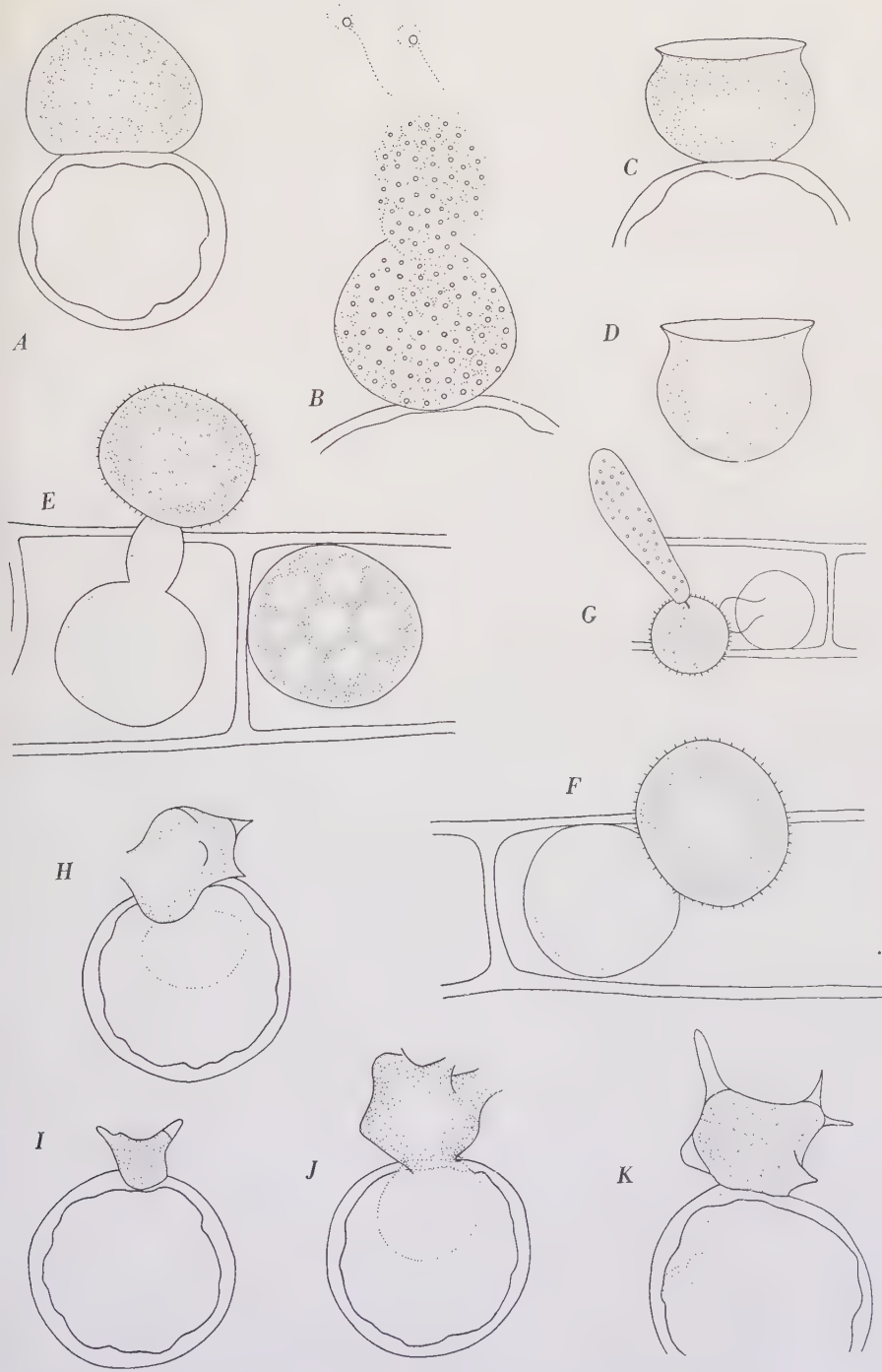
PLATE I

FIGS. *A–D. Rhizophydium sp.* on *Liquidambar* pollen. *A*, immature sporangium on pollen grain. *B*, discharging sporangium. *C–D*, empty urn-shaped sporangia. Figs. *E–F*, *Micromyces intermedia* on *Zygnema sp.* *E*, germinated prosorus with spiny sorus external to host cell. *F*, sorus showing lines of cleavage. *G*, *Phlyctidium sp.*, parasitic on sorus of *M. intermedia*. *H–K*, *Phlyctochytrium sp.*, on pollen. *H*, *J*, empty sporangia. *I*, *K*, undischarged sporangia. The endobiotic part of the fungus is only faintly visible.

Figs. *A–D*, *H–K*, × 700; Figs. *E–F*, × 1600; Fig. *G*, × 800.

PLATE I



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THE APPLICATION OF STATISTICS TO THE SEPARATION OF *SPHAGNUM MAGELLANICUM* BRID. AND *SPHAGNUM PAPILLOSUM* LINDB.

IRMA SCHNOOBERGER
Flint Junior College

The species of Sphagnum are extremely difficult to classify. Many characters are involved, such as presence or absence of fibrils in cortical cells of stems and branches; number of layers of cells in cortex of stem; presence or absence of pores in some or all cortical cells of stems and branches; shape and amount or place of exposure of chlorophyll cells; porosity of hyaline cells on inner and outer surfaces of branch leaves; shape and apical condition of stem leaves; degree of convexity of inner and outer surfaces of branch-leaf hyaline cells; and general pigmentation of the whole plant under consideration.

The application of statistical methods to the study of biological variation is not new. (Huxley, 1941, Tippett, 1950, Mayr, 1953). Consequently, I decided to apply statistical methods to certain characters of Sphagnum which lend themselves to such treatment and to ascertain whether these methods are of value for separating the species. Two species only are compared: *Sphagnum magellanicum* Brid. and *S. papillosum* Lindb., chosen because they are often quite difficult to separate specifically. Andrews (1913) considers them to be closely related, primitive species because of (1) their very wide distribution, (2) the central (primitive) position of chlorophyll cells in branch-leaf sections, (3) the fibrillose (primitive) condition of cortical cells of stems and branches, and (4) the lack of specialized marginal cells on branch and stem leaves. The key characters should separate them as follows:

A. Chlorophyll cells of branch leaves elliptic, ovate, or rectangular in section, entirely included or about equally exposed.
B. Chlorophyll cells in section oval, elliptic or broadly lenticular.

C. Chlorophyll cells small, elliptic, and usually entirely enclosed. *S. magellanicum*

CC. Chlorophyll cells usually broadly lenticular, inner walls thin and often papillose. *S. papillosum*

The designation "usually" causes trouble. To decide where to place a plant that has medium-length elliptic chlorophyll cells and lacks papillae is often difficult. One has to use other characters, such as number of pores in cortical cells or on the exposed surfaces of the hyaline cells of branch leaves. Andrews' (1913) comparison of descriptions for these species follows:

	Sphagnum magellanicum	*Sphagnum papillosum*
Stem:	outer cells of varying shape and size,	outer cells quadrilateral or somewhat irregularly shaped, often longer than wide,
	their pores rather large, round or often laterally elongate, 1 or 2 in each cell:	their pores rarely more than 1 or 2 in each cell, frequently small, always clearly defined:
Branch cortical cells:	outer wall frequently with a large round pore at the upper end:	outer wall often with a single large pore at the upper end:
Branch leaf hyaline cells:	on the inner surface with very few pores confined to the apical and lateral regions where they occur in the corners of the cells,	on the inner surface with small ringed pores in the cell-angles, and often in the apical and lateral portions of the leaf with large round pores in the central part of the cell, 1–5 per cell,
	on the outer surface with rather numerous large elliptic pores in the cell-corners and along the commissures, 4–10 per cell, fewer in short cells near the apex, passing into single membrane-gaps of the apex;	on the outer surface with rounded or elliptic pores in the corners and along the commissures, 4–10 per cell, passing into large membrane-gaps in the short cells of the cucullate apex;
Chlorophyll-cells:	elliptic in section, entirely enclosed or rarely slightly exposed on the inner or both surfaces,	truncately elliptic or nearly lenticular in section, usually about equally exposed on both leaf-surfaces,
	walls of the empty cells smooth;	walls of hyaline cells where overlying chlorophyl-cells densely and finely papillose, the papillae sometimes reduced or lacking;

These descriptions allow much leeway of choice to the experienced bryologist and may completely baffle the beginner. The following statistical procedure was designed in an effort to discover the range of variation in the characters of *Sphagnum* and the differences in their means between the two species studied.

Slides previously made from one plant from each of twenty-five collections of *Sphagnum magellanicum* and from thirteen of *S. papillosum* were used. From the slide of each plant, pore counts per cell were taken as follows:

(1) Surface of stem cortex where ten contiguous cells could be studied; (2) surface of branch cortex from middle portion of spreading branch where ten contiguous cells could be studied; (3) concave inner surface of branch leaf from broadest part of a spreading branch where ten contiguous cells were available; (4) concave outer surface of branch leaf from broadest part of a spreading branch where ten contiguous cells could be observed. Observations for (3) and (4) were taken from the third and fourth or fourth and fifth rows of cells above the base of the leaf. Since only thirteen collections of *S. papillosum* were available two different counts were made from each of the first twelve plants in order to have equal counts for the two species. The respective results are shown in Tables I, II, III, and IV.

To ascertain the value of pore numbers for separating *Sphagnum*

TABLE I

Comparison of Pores per Cell in Stem Cortex Cells of *S. magellanicum* and *S. papillosum*

Pores per Cell	*S. magellanicum*	*S. papillosum*	Total
0	22	6	28
1	191	160	351
2	34	72	106
3	3	12	15
	—	—	—
	250	250	500
Median	1.072	1.14	
Mean	1	1	

$\chi^2 = 27.78$ Degrees of freedom 3
$p < .01$

TABLE II

COMPARISON OF PORES PER CELL IN BRANCH CORTEX CELLS OF *S. MAGELLANICUM* AND *S. PAPILLOSUM*

Pores per Cell	*S. magellanicum*	*S. papillosum*	Total
0	70	53	128
1	180	197	377
	250	250	500
Median	1	1	
Mean	1.28	1.212	

$\chi^2 = 2.74$ Degrees of freedom 1
$.05 < p < .10$

TABLE III

COMPARISON OF PORES PER CELL IN BRANCH-LEAF CELLS, INNER SURFACE, OF *S. MAGELLANICUM* AND *S. PAPILLOSUM*

Pores per Cell	*S. magellanicum*	*S. papillosum*	Total
0	240	8	248
1	10	63	73
2		74	74
3		55	55
4		34	34
5		16	16
	250	250	500
Median	1	2	
Mean	.04	2.592	

$\chi^2 = 423.32$ Degrees of freedom 5 $p < .01$

magellanicum from *S. papillosum* the frequency distributions of pore numbers in the two species were compared by χ^2 for each of the four plant surfaces for which pore counts were taken, namely: stem cortex, branch cortex, typical branch-leaf inner concave surface, typical branch-leaf outer concave surface.

Andrews' description of stem cortex pores for *Sphagnum magel-*

TABLE IV

COMPARISON OF PORES PER CELL IN BRANCH-LEAF CELLS, OUTER SURFACE, OF *S. MAGELLANICUM* AND *S. PAPILLOSUM*

Pores per Cell	*S. magellanicum*	*S. papillosum*	Total
0	7		7
1	15	2	17
2	23	9	32
3	41	15	56
4	60	112	172
5	50	82	132
6	34	22	56
7	11	6	17
8	6	2	8
9	2		
10	1		
	250	250	500
Median	4	4	
Mean	4.876	5.548	

$\chi^2 = 59.42$ D.f. 8 (0–1 and 9–10 categories were grouped together).
$p < .01$

lanicum is "1 or 2 in each cell," for *S. papillosum* "rarely more than 1 or 2 in each cell." According to this, one would never expect to find pores lacking in either species. My observation revealed, however, that 22 of 250 cells of *S. magellanicum* lacked pores, and that 6 of 250 cells of *S. papillosum* lacked pores; 3 out of 250 cells of *S. magellanicum* had 3 pores, compared to 12 out of 250 cells of *S. papillosum*, which had 3 pores. *S. magellanicum* more often had 1 pore while *S. papillosum* more often had 2 pores. To summarize: *S. magellanicum* more often had 0, 1, or 2 pores while *S. papillosum* more often had 1, 2, or 3 pores (Table I). If one uses the average number of pores per cell from several plants of a collection it should be helpful in the diagnosis of the species.

The branch cortex pores are not diagnostic in separating the two species. Each usually has one pore per branch cortical cell (Table II).

The most significant diagnostic pore character of those studied is to be found in the relative number of pores on the inner surface of

hyaline cells from the concave area of typical branch leaves: *Sphagnum magellanicum* hyaline leaf cells on the inner concave surface never have more than 1, and usually none (mean = .04), but *S. papillosum* rarely has 0 and may have as many as 5, usually 1, 2, or 3 (mean = 2.592), (Table III). Relative number of pores per cell from this region counted in several leaves would be very diagnostic of any given specimen.

Branch-leaf, outer surface concave area, hyaline-cell pores are also diagnostic, but not so clearly diagnostic as are those of the inner surface. The range for *Sphagnum magellanicum* is 0–10 with 3, 4, or 5 most common (mean = 4.876), whereas that for *S. papillosum* is 1–8 with 4 or 5 most common (mean = 5.548). (Table IV). Again one should observe several leaves from the specimen before drawing a definite conclusion. In calculating the χ^2 for this distribution the 0–1 and 9–10 categories were grouped together—hence 8 degrees of freedom.

It has been recognized for some time that plants of a given species differ in their response to various environments (Dice, 1952).

Six of the collections of *S. magellanicum* came from a small bog in Washtenaw County and five from a small bog in Mecosta County and a comparison of the plants from the two regions was made (Tables V, VI, VII, VIII).

No significant differences were found for any of the plant structures observed. In this instance, this is a measure of similarity in

TABLE V

Comparison of Stem Cortex Pores of *S. magellanicum* from Washtenaw and Mecosta Counties

Pores	Washtenaw	Mecosta	Total
0	5	4	9
1	55	43	98
2		3	3
	—	—	—
	60	50	110
Median	1	1	
Mean	1.083	1.02	

p = .1916

TABLE VI

Comparison of Branch Cortex Pores of *S. magellanicum* from Washtenaw and Mecosta Counties

Pores	Washtenaw	Mecosta	Total
0	10	14	24
1	50	36	86
	—	—	—
	60	50	110
Median	1	1	
Mean	1.016	1.28	

$\chi^2 = 1.442$ $.20 < p < .30$ Degrees of freedom 1

TABLE VII

Comparison of Branch-Leaf Cell, Inner Surface, Pores of *S. magellanicum* from Washtenaw and Mecosta Counties

Pores	Washtenaw	Mecosta	Total
0	59	47	106
1	1	3	4
	—	—	—
	60	50	110
Median	0	0	
Mean	0.016	0.06	

$p = .3274$

the means and in variability of these characters in the plants. The plants came from two geographically separated localities. As such, the results add to confidence in the validity of the measures as a diagnosis of the species.

In many species of plants spores are of great value in classification. The spores of *Sphagnum*, however, have not generally been considered for this purpose for two reasons: (1) the plants are rather rarely collected with spores on them and (2) considering the whole group there is very little variety among the spores. There are years when most species in a bog will bear sporangia, but there will be

TABLE VIII

COMPARISON OF BRANCH-LEAF CELL, OUTER SURFACE, PORES OF *S. MAGELLANICUM* FROM WASHTENAW AND MECOSTA COUNTIES

Pores	Washtenaw	Mecosta	Total
0–1	0	4	4
2	3	1	4
3	7	7	14
4	16	9	25
5	15	12	27
6	12	10	22
7	6	3	9
8	1	1	2
9–10		3	3
	—	—	—
	60	50	110
Median	5	5	
Mean	5.2	5.2	

$\chi^2 = 6.292$ Degrees of freedom 8
$.50 < p < .70$

many years when only one or two, and sometimes none, will produce capsules. For this reason vegetative characters, which in *Sphagnum* can be studied in any season, are of much more use. Table IX is a record of spore sizes from capsules of *S. magellanicum* (seven plants) and *S. papillosum* (one plant). Of the many collections of each species in the University of Michigan Herbarium, these were the only ones bearing capsules, which emphasizes the scarcity of spore-bearing specimens.

The spore sizes are given in ocular micrometer spaces. To change to μ each should be multiplied by 3.6. The spores were placed on a slide in 10 per cent glycerin and allowed to stand twenty-four hours. Since some of the sizes recorded seemed large, a check was made by measuring spores of *Sphagnum magellanicum* which had been kept on a slide in water for twenty-four hours. The range was 7.0–9.5. Ten per cent glycerin was then added, and a second tabulation of sizes made after twenty-four hours. The range on the second measuring of the same material was 7.4–10.0. Apparently the glycerin causes the spores of *S. magellanicum* to swell. Thirty-

TABLE IX

TABULATION OF SPORE SIZES OF *S. MAGELLANICUM* AND *S. PAPILLOSUM*

Ocular Spaces	*S. magellanicum*								*S. papillosum*
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	Total	No. 1
6.0									3
6.1									1
6.2									1
6.3									3
6.4									3
6.5									5
6.6									4
6.7									4
6.8									9
6.9									12
7.0									29
7.1									15
7.2									7
7.3									7
7.4									6
7.5	2	5	2					9	6
7.6									6
7.7									6
7.8									6
7.9									5
8.0	11	9	20	10	8	7	18	83	8
8.1		1	7		2	1	9	20	3
8.2	2	4	1	1	2		3	13	1
8.3							2	2	
8.4		1					1	2	
8.5	7	3	2	4	2	4	1	23	
8.6						1		1	
8.7									
8.8				1	2	1		4	
8.9					1			1	
9.0	10	9	4	16	17	17	1	74	
9.1					2	1		3	
9.2				2				2	
9.3									
9.4									
9.5	2	1		1		1		5	
9.6									
9.7									
9.8				1		1		2	
9.9									
10.0	2	3				2	1	8	
	36	36	36	36	36	36	36	252	150
Mean	8.597	8.52	8.15	8.71	8.67	8.83	8.17	8.53	7.19
F	210.8	177.15	134.93	285.64	275.31	319.81	141.72	8.608*	

* Highly significant.

TABLE X

ANALYSIS OF VARIANCE OF SPORE SIZE BETWEEN AND WITHIN SEVEN INDIVIDUALS OF *S. MAGELLANICUM*

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square
Between individuals	14.22	6	2.37
Within individuals	67.46	245	.2753

F = 8.61 .01 > p

six spores from each of seven capsules of *S. magellanicum* and 150 from one capsule of *S. papillosum* were measured (Table IX).

An analysis of variance of spore size was applied to the differences between and within the seven specimens of *S. magellanicum*, as is shown in Table X. The differences between individual plants were highly significant.

Analysis of variance was also employed in comparing the spore sizes of the specimen of *S. papillosum* successively with each of the seven specimens of *S. magellanicum* as is shown in Table XI. Each specimen of *S. magellanicum* was found to differ significantly in spore size from the specimen of *S. papillosum*. However, the smallest average spore size for *S. magellanicum* was less different from the largest average spore size of *S. magellanicum* than it was from the average spore size of *S. papillosum*.

SUMMARY

On the basis of the material studied:

1. In differentiating *S. magellanicum* from *S. papillosum* a tabulation of the pore number per cell of a sufficient number of contiguous stem cortical cells is significant and useful, *S. magellanicum* cortical cells usually having 0–1 pore and *S. papillosum* usually having 1–3 pores.

2. The comparison of number of pores in branch cortical cells of the two species is not useful in separating these species.

3. The best distinction between these two species is found in number of pores on inner walls of contiguous hyaline cells from the most concave region of a typical branch leaf. There is a very significant difference in pore number per cell from this region of branch

TABLE XI

ANALYSIS OF VARIANCE OF SPORE SIZE BETWEEN AND WITHIN THE SPECIMENS OF *S. MAGELLANICUM* AND THE SPECIMEN OF *S. PAPILLOSUM*

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square
SPECIMEN NO. 1			
Between individuals	56.81	1	56.81
Within individuals	49.59	184	.2695
F = 210.8 .01 > p			
SPECIMEN NO. 2			
Between individuals	51.51	1	51.51
Within individuals	53.50	184	.29076
F = 177.15 .01 > p			
SPECIMEN NO. 3			
Between individuals	29.48	1	29.48
Within individuals	40.20	184	.21847
F = 134.93 .01 > p			
SPECIMEN NO. 4			
Between individuals	69.64	1	69.64
Within individuals	44.86	184	.2438
F = 285.64 .01 > p			
SPECIMEN NO. 5			
Between individuals	65.34	1	65.34
Within individuals	43.67	184	.23733
F = 275.31 .01 > p			
SPECIMEN NO. 6			
Between individuals	80.42	1	80.42
Within individuals	46.27	184	.25146
F = 319.81 .01 > p			
SPECIMEN NO. 7			
Between individuals	31.24	1	31.24
Within individuals	40.56	184	.22043
F = 141.72 .01 > p			

leaves of the two species: *S. magellanicum* has 0–1, while *papillosum* has 0–5 with 3, 4, or 5 most common.

4. The pores on outer walls of contiguous hyaline cells from the most concave region of a typical branch leaf are also differential, in that cells of *S. papillosum* never lack pores and do not exceed 8 pores per cell (usually have 4), while cells of *S. magellanicum* sometimes lack pores and may have up to 9 or 10 per cell (usually 3, 4, or 5).

5. Comparison of collections of plants from two geographically separated localities are not significantly different, thereby adding to confidence in the validity of the measures as a diagnosis of the species.

6. The spores of *S. magellanicum* and *S. papillosum* differ enough in size to be distinctive for each species, and when available are of value in separating them. The spores of *papillosum* average appreciably smaller than those of *magellanicum*.

7. Statistical methods promise to be of much aid in the identification of the numerous elusive species of *Sphagnum*. Certainly further studies should be made on the feasibility of using spores to differentiate species whose vegetative structures or color are a somewhat uncertain or unreliable means of identification. While the spore sizes of many of the species are very much the same, it is possible that a consistent though slight difference in spore size between two species otherwise very similar, if taken into consideration in conjunction with the special markings or color of the spores, might help materially in separating the species.

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FORESTRY

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PLOT SIZE IN FOREST GENETIC RESEARCH

JONATHAN W. WRIGHT AND F. DEAN FREELAND, JR.
Michigan State University

Introduction

In the beginning stages of a forest genetics program a researcher must test scores of different individual tree progenies, clones, ecotypes, or species—sometimes hundreds. It is not difficult to conduct a 100-origin nursery test consisting of four replications of 100 seedlings each—or a total of 40,000 seedlings. But outplanting these 40,000 seedlings is more expensive. And it is extremely expensive to measure these 40,000 trees after they have grown 30 or 40 feet. Frankly, we would prefer not to have anything to do with the 40,000 trees if we could find an experimental design that would yield equal or better results with 1,000 or 2,000 trees.

The uniformity trial—on which we shall report here—is one approach to the program of experimental efficiency. Uniformity trials have been conducted on several agricultural crop plants (Keller, 1949; Fleming *et al.*, 1957). Most of the uniformity trials have shown that small plot experiments are most efficient.

Procedure

Two plantations were chosen for study. Both had been established with ordinary commercial seedlings. In each the genetic variability was distributed uniformly through the planting.

The first was a red pine planting in Section 34, Ingham Township, Ingham County, Michigan, on gamelands owned by the Michigan Department of Conservation. Mortality had been relatively low. The site was typical of many sites available for test plantings in southern Michigan, with level to rolling topography and maximum slopes of about 5 per cent. On the higher portions the 6-year-old (since outplanting) trees were from 4 to 8 feet tall, and in the lower, swampy portions they were from 2 to 5 feet tall.

The planting consisted of 50 rows of seven trees each. There was no noticeable border effect, and the heights of all trees were measured to the nearest tenth of a foot. In the laboratory these measurements

were treated as if the planting had consisted of 350 1-tree plots, 175 2-tree plots, 50 7-tree plots, and so on. For each set of plot means the between-plot variance was computed from the following formula:

$$V = \frac{\epsilon X^2/n - (\epsilon X)^2/nr}{r}$$

Where V = between-plot variance, X = average plot height, n = number of trees per plot, and r = number of plots or replications. We used r rather than (r-1) because we were dealing with the universe of 350 trees rather than with a sample.

To calculate the relative statistical efficiency of n-tree plots in terms of 1-tree plots we used the formula

$\frac{V_1}{V_n}$ = efficiency, where V_1 and V_n are respectively the plot-sum variances of 1- and n-tree plots.

The number of replications needed to show significance of a certain difference between varietal means was calculated according to the formula

$$t = d/\sqrt{V2/r},$$

which reduces to

$$r = 8V/d^2$$

if t = 2 = Students' t, V = variance, r = number of replications, and d = minimum detectable difference.

The second stand studied was a yellow-poplar (*Liriodendron tulipifera* L.) plantation on Michigan State University's Russ Forest in southwestern Michigan. It was established in 1941 on a 6 by 6 foot spacing, and now contains 5- to 30-foot trees. In topography and surface soil the planting site was as uniform as could be found in southern Michigan. The diameter of every tree on an interior 32 by 32 tree square was measured. The measurements were treated statistically in the same manner as described for red pine.

There were small numbers of missing trees in both plantings. In the statistical analyses all plots on which half or more of the trees were dead were eliminated from consideration. If the majority of trees on a plot were alive we substituted a value equal to the plot mean for each missing tree. The only theoretical consideration involved in this adjustment was that the missing trees would have grown similarly to live trees on the same plots.

TABLE I

RELATIONSHIP BETWEEN PLOT SIZE AND EXPERIMENTAL EFFICIENCY IN RED PINE

Plot Width × Length	Trees per Plot	Relative Information	Replications Needed*
Trees	Number	Per Cent	Number
1 × 1	1	100.0	100
2 × 1	2	79.3	63
4 × 1	4	51.2	49
5 × 1	5	49.5	40
1 × 7	7	33.1	43
2 × 7	14	28.8	25
4 × 7	28	11.7	30
5 × 7	35	12.2	23

* To show significance of a 0.34 foot difference in height between progeny means.

TABLE II

RELATIONSHIP BETWEEN PLOT SIZE AND EXPERIMENTAL EFFICIENCY IN YELLOW POPLAR

Plot Width × Length	Trees per Plot	Relative Information	Replications Needed*
Trees	Number	Per Cent	Number
1 × 1	1	100.0	100
1 × 2	2	85.4	58
2 × 1	2	86.6	58
1 × 4	4	61.2	41
4 × 1	4	75.6	33
2 × 2	4	60.7	41
5 × 1	5	54.6	37
2 × 4	8	38.0	33
4 × 4	8	42.8	29
5 × 2	10	21.8	46
4 × 4	16	27.3	23
4 × 8	32	22.6	14
8 × 4	32	19.4	16
8 × 8	64	18.5	8

* To show significance of a 0.29 inch difference in diameter breast high between progeny means.

Results

The results are given in Tables I and II. There was rapid decrease in statistical efficiency or relative information with increasing plot size. This decrease was most pronounced in red pine because that was on a noticeably variable site. The red pine results indicate that a varietal test composed of 23 35-tree plots per variety (805 trees per variety) would give the same statistical precision as a varietal test composed of 100 1-tree plots per variety (100 trees per variety). In other words, the large plot experiment would result in 8 times the effort required for the small plot experiment.

The rapid decrease in statistical efficiency in the yellow-poplar study is especially noteworthy because this stand was situated on so uniform a test site. If yellow poplar were to be tested on a more variable site, the statistical advantages of small-plot experiments would be even more pronounced.

Conclusions

The statistical superiority of much replicated, small-plot experiments has been demonstrated by Fleming *et al.* (1957), Keller (1949), and many other agronomists. Forest tree breeders, however, have continued to use relatively inefficient 50-, 100-, or 200-tree plot designs for two reasons. First, there have been only two previous papers giving comparisons between plots of different sizes (Strand, 1952; Wright and Baldwin, 1957). This paper is the first attempt to assign numerical values to the relative efficiencies of experiments involving several different plot sizes. Second, tree breeders have been prone to subordinate statistical to other considerations. Actually, statistical significance should always be considered first. Why bother to explain the differences in branch habit between varieties A and B if there is no proof that A and B are different?

Mortality and resultant missing plots are sometimes used as a reason for not using small plot designs. But small numbers of missing plots are not serious. They can be treated in several ways. With 10 per cent mortality an increase from 1 to 2 trees per plot will reduce the number of missing plots from 10 to only 1 per cent. There are standard procedures for computing missing plot values for insertion in an analysis of variance. These methods are laborious but statistically valid. If differences among replicates are slight, between-replicate variance and the missing plots can be ignored in the analysis

of variance. If most of the missing plots occur in one replicate that replicate can be omitted from the variance calculations. If most of the missing plots occur in one variety, that is good. We can perform an analysis of variance on the mortality data and forget about the growth of that variety.

Actually, there is no excuse for having more than 10 per cent initial mortality in a field test. Establishment costs are a small percentage of total experiment costs, and reasonable precautions such as clearing brush, plowing sod, planting larger-than-usual stock, and replacing first-year mortality should be practiced if there is any reason to believe that first-year mortality will be large.

The need for testing trees in competition with other trees of similar genotype is frequently given as a reason for the use of statistically inefficient 49-tree or larger plots in which the majority of the trees occupy interior positions. During its first 10 or 15 years a plantation is little more than a collection of individual open-grown trees. What difference in growth will the planting arrangement make, especially if the growth rate difference between the best and the poorest progenies is only 10 per cent, as will be true in most single-tree selection studies? Only two important tree characteristics on which we desire genetic information—self-pruning ability and bole form factor—must be tested under forest conditions. Differences in height growth, diameter growth, branch diameter, bole straightness, and pest resistance can be determined in open-grown trees. Thus, insistence on large-plot designs will usually result in lowered statistical efficiency and increased costs but not in increased information.

A 1- or 2-tree plot experiment must be thinned by the removal of entire plots. Say the thinning intensity is 75 per cent. The final stand will contain all of the best progenies (25 per cent of the original plot) and none of the poorest progenies (75 per cent of the original plot). Genetically, this is advantageous because it gives full information about the best progenies from beginning to end and because it reserves all trees of the best progenies for use as breeding stock. Future tree breeders will be too busy with good progenies to use poor progenies as parents.

Cost should be mentioned. As trees get older they get taller and more difficult to measure. At age 50 a 10,000-tree red pine experiment may well cost $10,000 to measure. It should not be planted if it is not going to be measured properly. How much better it would

be to make that $10,000 give the same quality of answers for 10 species rather than for one species.

Summary

We conducted uniformity trials on red pine and yellow-poplar plantations in southern Michigan. In both species there was a rapid decrease in statistical efficiency with increasing plot size. For example, 35-tree red pine plots were only 12 per cent as efficient as 1-tree plots. Provided that test plantings are carefully established, the use of small plot designs is also advantageous from the cost and thinning standpoint, and poses no special missing plot or competition problems.

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ARE WATER TABLE LEVELS AN IMPORTANT FACTOR IN THE ESTABLISHMENT AND GROWTH OF YELLOW BIRCH?

R. M. GODMAN
Lake States Forest Experiment Station, Marquette, Michigan

The influence of ground water levels has received only indirect and superficial attention in forest management. Soil moisture and distribution of precipitation are indicators of the moisture regime more commonly used. But they are not always indicative of the water table fluctuations. When the effect of water table levels on timber stands has been considered, it has been mostly in reference to droughts or extreme low levels. In yellow birch stands in the Upper Peninsula of Michigan, water tables have recently been investigated as a factor in the growth and development, particularly the top-dying and regeneration, of this species. Recent studies and observations of this problem, especially for extended periods of high water tables, are reported in this paper.

In the Upper Peninsula, yellow birch has the highest value of any tree species, but it is (1) one of the most difficult to establish and grow to maturity, (2) more intolerant than the associated species in the types where it normally occurs, and (3) more exacting in its seedbed requirements. Throughout the Peninsula, similar appearing stands cut in the same manner generally show inconsistent results in the composition of reproduction and the amount of yellow birch. A major problem in older stands is heart rot, which may be related to the top-dying that has been observed in this area. Slow growth rates in some localities is also a problem. Part of these difficulties may be associated with fluctuations of the ground water levels.

Available Records on Ground Water Levels in Upper Michigan

Records on ground water levels are exceedingly limited. Available information is mainly from wells associated with municipal or industrial uses, and they are often affected by pumpage. Many of them have only short or intermittent periods of record. The longest

records available for study are a series of wells established in 1945 by the Wisconsin Michigan Power Company. In addition to the regular monthly measurements, data were also taken during expected extremes. Although many of these wells are in coarse, well-drained soils supporting pine types, their records do provide a comparison of annual water table fluctuations.

Although a few measurements of ground water levels were taken in temporary wells on the Upper Peninsula Experimental Forest shortly after its establishment in 1926, no systematic records were made until a series of recording wells were dug in 1954 and 1955. These consisted of five shallow wells installed in five different timber stands to obtain preliminary information on the amount of water level fluctuation associated with different timber types. They were hand-dug to depths of from 3 to 6 feet and lined with sheet metal tubing.

Since then continuous water level records have been kept during the growing season. During the winter, systematic measurements could not always be made because the deep snow made some stations inaccessible. The data, however, show the general relationships of forest type, regeneration, and growth with water table depth.

Association of Forest Cover Types with Water Table Levels

Figure 1 illustrates the seasonal fluctuations of the water table under five different timber stands of three forest cover types during the 3 years observed. Under the mixed coniferous swamp type the water level was near the ground surface throughout most of the growing season and showed relatively little change. Under the pure sugar maple type, with essentially no yellow birch in the stand, the ground water was commonly below the 4½-foot level.

Ground water levels in the hemlock-yellow birch associations were intermediate in depth between the pure sugar maple and the mixed coniferous swamp, but varied with the degree of cutting and topographic position. The stand designated A is uncut and on a uniformly flat area. Stand B is also uncut but is on a bench near the foot of a moderate slope. Below this stand the type changes to lowland hardwood and patches of mixed coniferous swamp.

The hemlock-yellow birch stand C is near the highest point of the Experimental Forest, with the observation well on a very gentle south slope. The area was heavily cut as part of a yellow birch regenera-

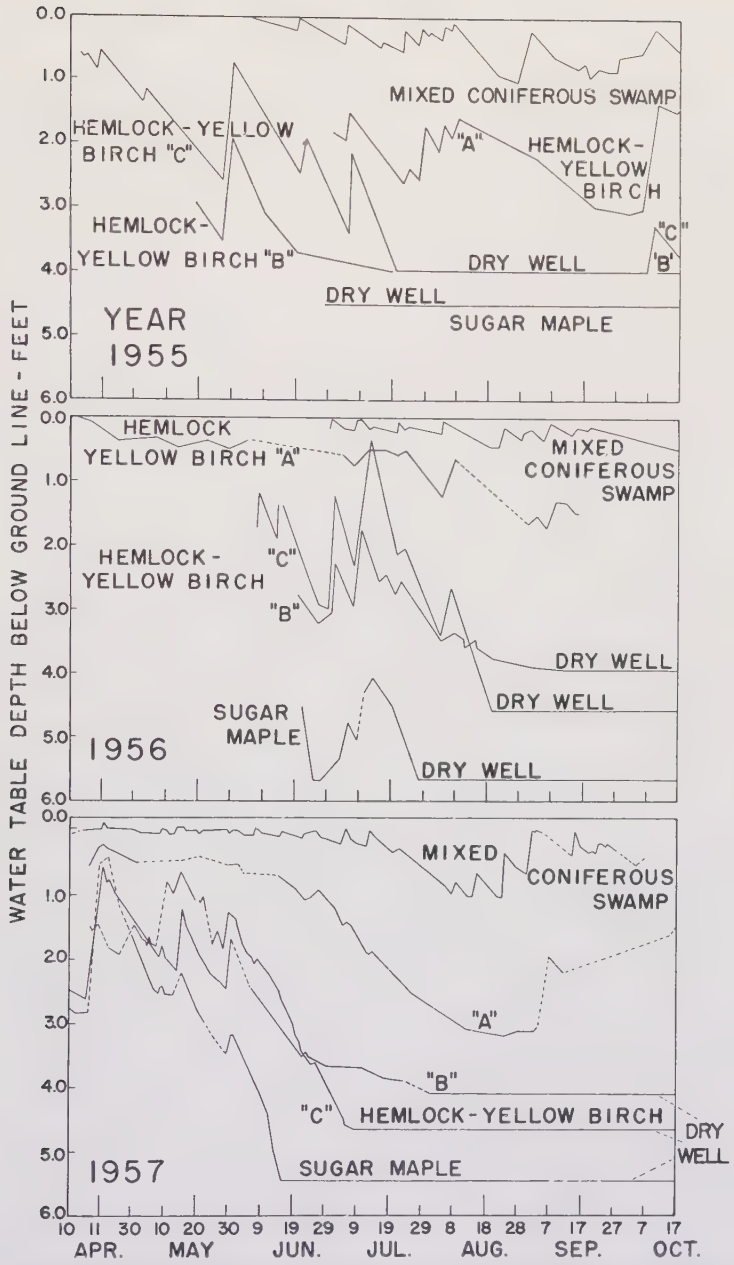

FIG. 1. Water table fluctuations under different forest types, Upper Peninsula Experimental Forest, 1955–57.

tion study 2 years before the ground water well was established. The per-acre average of the residual stand was 21 trees 10 inches and larger in diameter at breast height. Before cutting, yellow birch constituted 25 per cent of the 15 thousand gross board feet per acre, which is similar to stands A and B.

The highest water levels in all stands occurred during the period of snow melt in early April; this was followed by a general decline, interrupted only temporarily by heavy rains. The late spring peaks were usually of short duration. During the 3 years of record annual precipitation was below the normal of 33½ inches. In 1955 and 1957, the ground water levels remained high for only a short period. In 1956, however, the high levels remained well into July, probably because the precipitation from April through July that year was slightly above normal. Precipitation for the same period in 1955 and 1957 was 64 and 79 per cent of normal.

Between the timber stands there is a general seasonal trend of water table fluctuations. The low levels frequently occur at approximately the same time, but the peaks often have a time lag that varies with the cover type. In the heavily cut stand C, greater and more rapid fluctuations occurred as the result of the decrease in stocking.

Influence of Water Table Levels on Regeneration

The establishment of yellow birch reproduction, which is one of the major problems in the management of yellow birch, appears to be dependent on soil moisture conditions as well as seedbed preparation. Burton (2) and Linteau (7) found in Canada that unfavorable seedbeds were the principal causes of failure of yellow birch to reproduce. A study of seedbed conditions on the Upper Peninsula Experimental Forest indicates that high water levels tend to improve the suitability of seedbeds. The study, begun in the fall of 1952, concerned the effect of mechanical scarification of the seedbed in the hemlock-yellow birch stand designated as C. A heavy cutting removed all seed-bearing trees except yellow birch. In the fall of 1953, half of the area was partly disked. Reproduction was systematically sampled for the whole area on 400 ¼-milacre quadrats.

Results in the fall of 1956 (6) showed that the greatest number and best growth of yellow birch reproduction occurred on quadrats that had 75 per cent of their area disked. On less favorable seedbeds, the number of seedlings varied considerably.

The effect of moisture was most apparent where there was no

disking. Considering the undisked areas alone, the average number of yellow birch seedlings was 31 thousand per acre. In low areas where the water table stayed at or near the surface throughout most of the growing season, more than 80 thousand yellow birch seedlings per acre had become established 3 years after the cutting. In most instances these seedlings were competing with herbaceous ground cover, including thick mats of grasses. Although their development was somewhat retarded, their chance of survival and continued development appears to be very good.

On slightly higher and drier portions, very little yellow birch survived on the undisked areas if there was competition.

Influence of Water Table Levels on Diameter Growth

Data describing the effect of water tables on diameter growth are very limited in the Upper Peninsula and adjacent areas. In 1956 Fraser (3) reported the annual and seasonal growth of several tree species in Ontario by soil moisture regimes. Seasonal radial increment for yellow birch decreased as the sites became wetter. The water table levels associated with these moisture regimes are given in a later report by Fraser (4). Although the variations in growth between years were not completely correlated with water level, there appears to be good evidence that it exerts an influence on diameter growth. Fraser states that "Growth of most trees will be impeded if the soil is drier than the permanent wilting percentage or wetter than field capacity."

The effect of high water levels on diameter growth was observed on two experimental cutting plots on the Upper Peninsula Experimental Forest. Both plots were cut by a group selection method. One has a very high water table varying from 0 to 5 feet during most of the growing season, and the other has a deep water table averaging more than 15 feet. Average diameter growth of yellow birch was 0.2 inch less during a 5-year period after cutting on the plot with the higher water table even though the stocking between the openings was slightly less than on the other plot.

Association of Water Table Levels with Top-Dying of Yellow Birch

Extended periods of high water table levels are apparently unusual in the Upper Peninsula. During 1949–57, this situation occurred only in 1954, according to the records of the Wisconsin Michi-

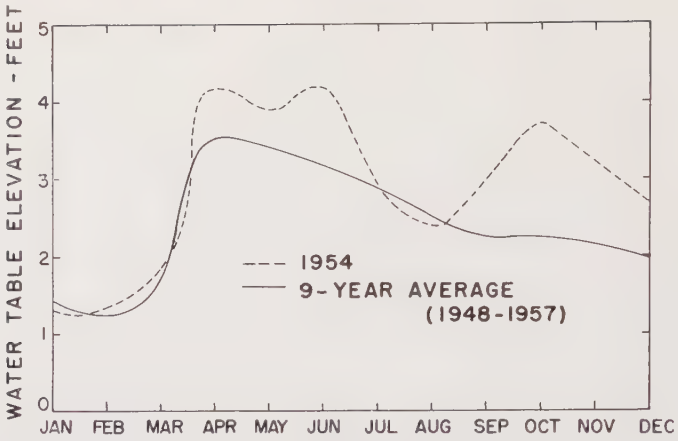

Fig. 2. Water table fluctuations of 34 wells above a mean depth in the Menominee River Basin, 1954 and 1949–57. From Wisconsin Michigan Power Company data (8, 9).

gan Power Company (Fig. 2) (8, 9). Weather data for that year in central Upper Peninsula show that cumulative precipitation for the months of April, May, June, and July was 195, 152, 127, and 104 per cent, respectively, of normal. The high water table levels extended into early July, rather than declining after early May. The levels maintained were nearly as high as the maximum peaks of other years. The same year this unusual condition occurred, dead tops were observed in a high percentage of yellow birch in late May and June (5).

Damage ranged from slight discolorations of the foliage to death of the trees. The injury occurred almost as frequently in uncut stands as in those that had been cut over. In all stands, however, the trees are now showing a trend toward recovery, with the virgin and lightly cut stands improving at a greater rate. This type of injury had been observed on individual yellow birch trees in the past without causing appreciable differences in growth.

A similar condition of top-dying of paper birch and yellow birch in the eastern United States and Canada, called dieback, has been investigated by many researchers. Several of them have suggested that extremely dry weather may be the initial cause of dieback. The Wisconsin Michigan Power Company data for 1949–57 show only 1 year of abnormally low ground water levels. This occurred in 1949, but no top-dying was observed in the Upper Peninsula.

Braathe (1), analyzing the literature on birch dieback, has the opinion that dry weather was not an important cause. He suggests that the March thaw of 1936, which caused the heaviest flood known in the St. John River in New Brunswick, Canada, may be intimately associated with the dieback.

The physiological effect of high water tables on yellow birch is not precisely known. It has been suggested that the primary effect is the reduction of available oxygen to the sensitive feeder rootlets. Other effects may include the lowering of soil temperatures that seriously retard the absorption of water and mineral nutrients.

Summary

The available data, though limited, indicate that water table levels are a factor in the regeneration and development of yellow birch. They appear to be associated with the species distribution and the growth and development of the stands, and may exert either a beneficial or detrimental effect, depending on the duration of water table extremes.

In mature uncut stands in the Upper Peninsula, yellow birch is usually associated with mesophytic species, including hemlock, red maple, basswood, and American elm. As the drainage improves and the water table lowers, there is a transition from this type to the sugar maple association where the proportion of yellow birch is smaller. The ground water levels associated with this transition, however, are dependent to some extent upon the soil texture and its water-holding capacity.

Yellow birch regeneration is usually greatest on mineral soil seedbeds. On undisturbed seedbeds high water tables may provide the necessary moisture to establish the reproduction. However, in older stands, high water tables may be less favorable for growth. Furthermore, extended periods of high water tables may result in injury to the crowns.

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